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OBSERVATIONS ON THE INFLORESCENCE OF APOCYNACEAE

(With Special Reference to the American Genera of Echitoideae)

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Introduction

As one reviews the advances of plant morphology during the past quarter century and more, one can scarcely avoid recognition of the fact that systematic botanists have made few recent contributions of note to our practical and theoretical knowledge of the structure of plants. This is in spite of the fact that the whole superstructure of plant classification rests upon an intimate knowledge of such considerations. The situation is incongruous with the superior opportunities which systematists enjoy for the advancement of the very basic and elemental science of plant morphology.

In the monographic method of investigation, the systematist has developed a tool of the very greatest potentiality for the exhaustive investigation of the morphology of plants. The accumulating multitudes of specimens in the great herbaria of the world which are available for study, particularly by the trained systematist, constitute an unsurpassed field for observations concerning the known flora in its entirety with the greatest ease. The important investigations of Solereder and

others upon the anatomy of flowering plants toward the close of the past century should remind us that herbarium specimens are capable of more uses in botanical research than ordinary dissection for the purpose of identification.

The possibility of studying the inflorescence of Apocynaceae largely by means of herbarium specimens was first appreciated by the present writer while studying in the Royal Botanic Gardens and herbarium at Kew during the summer months of 1930. The accurate picture of inflorescence structure which such specimens are capable of revealing was manifest at that time upon comparison of the exsiccatae with the abundant flowering material of *Allamanda Schottii* Pohl found in the conservatories containing *Victoria regia* and other tropical species. The gardens at Kew are perhaps the richest in cultivated species of Apocynaceae among the botanical gardens of the world, and the preliminary comparison of desiccated and living specimens of numerous genera of the family found there, made possible through the courtesy of the Director, Sir Arthur W. Hill, and others in authority, has proved of the utmost value in the subsequent studies of the inflorescence of which this paper is a condensed report. Since the commencement of the problem at Kew, the writer has continued the study of the apocynaceous inflorescence in the herbarium and living collections of the Missouri Botanical Garden at St. Louis.

The taxonomy of the Apocynaceae has claimed my attention for nearly a decade during which I have examined thousands of specimens of this family deposited in the principal herbaria and botanical gardens of America and Europe. The Apocynaceae are divisible into three subfamilies, the Apocynoideae, the Echitoideae, and the Plumeroideae. The scope of my taxonomic studies has included all the recognized genera and species of Apocynoideae and Echitoideae indigenous to the western hemisphere, as well as certain related genera of Europe and Asia (Woodson, 1930, 1933). Earlier studies have also included certain genera of Plumeroideae (Woodson, 1928a, b).

Structural advantages of the flowers of Apocynaceae which overcome the disadvantages suffered by desiccation to an appreciable extent in investigating the gross morphology of the

inflorescence can be indicated at this time. The flowers of the family as a whole are large, permitting even relatively small discrepancies of age to be visible in the development and size of the buds. The rule of large flowers is broken in such genera as *Forsteronia* and *Apocynum,* but even in such instances difference in stages of development of the floral buds is clearly indicative of correlated age and potential time of blooming, very important factors in the interpretation of modes of inflorescence. Relative age of floral members is also manifest in young fruit. A less obvious criterion in this connection is found in the accrescence of the pedicels. Since the pedicels increase in length and diameter for some time preceding abscission, even in the case of flowers which have failed of fertilization, a third important clue is present in herbarium, as well as in living, specimens to enable us to determine the phenology of the inflorescence with some precision.

The range of inflorescence structure exhibited throughout the family Apocynaceae comprises nearly all the more familiar types found among the flowering plants with the exception of such specialized examples as the capitulum and the ament. The most common inflorescence is the cyme, particularly the dichasium. At this juncture it becomes necessary to outline briefly the characteristic types of inflorescence amongst the Apocynaceae, both as a hasty survey and as a definitive introduction to the succeeding discussion. It will be found that the definitions of the inflorescence follow closely those of Jackson (1900).

Dichasium.—The dichasium is the most familiar type of cymose inflorescence throughout the flowering plants. It consists of a solitary flower terminating the primary axis of the stem or branch. Subtending this flower are normally two opposite leaves or bracts in the axils of which arise two secondary branches, each terminated by a flower similar to the first, but blooming subsequently and usually simultaneously. Such an axis system is called a simple dichasium. A continuous, or compound dichasium is frequently observed in the branching of the secondary axes in a manner similar to that of the primary, and so on. Such subsidiary components of a compound cyme are designated by the diminutive *cymule.* Dichasia are

frequently so composed of innumerable flowers arranged in impressive regularity. This type of inflorescence is found in numerous genera of Apocynaceae, including *Cycladenia* Benth., *Rhabdadenia* Muell.-Arg., and *Echites* P. Br.

Aggregate Dichasium.—A "panicle" is strictly defined as a compound inflorescence all axes of which are indeterminate. This interpretation was original with Roeper (1826), to whom we owe the first thorough-going discussion of the inflorescence. Nevertheless the general use of the term, persisting since the time of Linnaeus, still permits its use for virtually any compound inflorescence, preferably pyramidal and "loose" (Jackson, 1900; Gray, 1907).

The exact opposite of paniculate construction, one in which all axes of a compound inflorescence are determinate, has apparently never received a generally accepted name, although it, too, frequently is made to masquerade as a "panicle." This type of compound inflorescence differs from the typical dichasium in that although the latter is the ultimate constituent of its construction, more than a single pair of branches occur, ordinarily at regular, decussate intervals below the determinate flower of the primary axis (cf. text-fig. 3, A). For want of a better name it is called an *aggregate dichasium,* since the inflorescence itself consists properly not of a single dichasium but of an aggregation, just as a raceme consists not of a single flower, but of an indefinite collection of them upon a specialized shoot. This type of inflorescence is conspicuous among Apocynaceae, as well as in certain other families, as Gentianaceae, being well organized in such familiar genera as *Apocynum* L., and *Forsteronia* G. F. W. Meyer,[1] accounts of which follow shortly.

Cincinnus and Bostryx.—In those cymes which consist of a single, sympodial axis, the monochasia of Eichler (1875), derivation from a dichasium has long been assumed by the substitution of a single flower for one of the equivalent inflorescence

[1] The limitations of publication preclude a complete category of the inflorescence structures of the genera of Apocynaceae which number at the present time more than two hundred.

branches. A bostryx is formed when the remaining subsidiary axis of such a modified dichasium is always either to right or to left of the determinate flower. This usually results in the somewhat curled inflorescence known as "helicoid," familiarly represented in many Boraginaceae. The maintenance of branching of such a highly modified dichasium alternately to right and to left, resulting in a somewhat zigzag sympodium widely known as "scorpioid" is characteristic of the cincinnus. In the bostryx and the cincinnus the sympodium is usually more or less curled or zigzag respectively. They may be simple throughout, or variously branched, by which they may recall their dichasial ancestry to a certain extent. Not infrequently the axis may become quite straight, however, when the nature of the sympodium must be distinguished by the usually paired pedicels in the axil of a single bract which is opposed to an "empty" bract upon the other side of the peduncle (cf. pl. 3, fig. 3). The peduncle is literally in the axil of the "empty" bract, which frequently becomes greatly dislocated in highly modified scorpioid and helicoid cymes, rendering their interpretation less easy.

The bostryx and the cincinnus occur widely throughout the Apocynaceae, the former in such genera as *Odontadenia* Benth., *Allamanda* L., and *Asketanthera* Woods., and the latter in *Prestonia* R. Br., *Temnadenia* Miers, and *Mesechites* Muell.-Arg. Scorpioid and helicoid modifications frequently creep into the ramifications of other cymose types, particularly when multiflorous.

Raceme.—Scarcely distinguishable from some highly modified examples of superficially indeterminate scorpioid and helicoid cymes is the truly indeterminate raceme. A typical raceme may be defined as a simple, pluriflorous, monopodial inflorescence in which a solitary pedicel is borne in the axil of a single bract. A pronounced peduncle is usually present which is of relatively greater length than the individual pedicels. Familiar modifications of the typical raceme are the spike, the corymb, and the umbel, based upon the relative length, or essential suppression of peduncle and pedicels. Typical racemes are infrequent in Apocynaceae, the principal genus bear-

ing them being *Mandevilla* Lindl., of some 108 species of the western hemisphere.

Jackson (1900) defines the umbel as "properly indeterminate," but recognizes the use of such a term as "cymose umbel" for those which are centrifugal and not centripetal in their floral development. Similarly, the same authority defines both a spike and a corymb as indeterminate. In these cases also it appears inevitable to recognize determinate as well as indeterminate spikes and corymbs. In such species as *Forsteronia paludosa* Woods., it will further be necessary to deal with a spiciform thyrse: a typical thyrse in which the pedicels are suppressed. Corymbs, in their typical, indeterminate sense, are restricted to racemose genera, as in *Mandevilla callacatensis* Mgf. The true umbel in Apocynaceae is unknown to this writer. Cymose, or determinate, corymbs and umbels are widely observed in such genera as *Prestonia* R.Br., *Thenardia* HBK., *Malouetia* A.DC., and *Asketanthera* Woods.

The spike, the umbel, the corymb, and other similar types, are doubtless merely modes of more fundamental types of inflorescence, and it would appear more simple in the end to use them in an adjectival manner, such as "corymbose raceme," and "corymbose cyme," than to limit the use of the word "corymb" to an indeterminate structure, in which case there would be an obvious necessity for another word to express similar, but determinate construction.

Thyrse and Panicle.—The thyrse and the panicle are recognizable as compound inflorescences in which the primary axis is indeterminate. In the true panicle, as represented by the common lilac, *Syringa vulgaris* L., the subsidiary axes, whatever their number, are likewise indeterminate. In the thyrse, however, the ultimate ramifications of the inflorescence are determinate, hence the "mixed inflorescence" of A. P. De Candolle (1827). The modification of the thyrse is excellently shown in the apocynaceous genus *Forsteronia*, amongst others, in which the determinate construction is variously expressed upon branches of differing magnitude throughout the entire inflorescence. The true panicle apparently is not found in any known Apocynaceae, although it is approached in certain species of

Forsteronia, a detailed account of which is reserved for succeeding paragraphs.

Solitary Flowers.—Solitary flowers are found in both terminal and lateral positions in the Apocynaceae. The former is typical of such genera as *Salpinctes* Woods., and such exceptional species of predominantly pluriflorous genera as *Echites crassipes* A. Rich. In all known instances, however, very inconspicuous, subtending bracts are usually capable of detection. In the familiar creeping myrtle, *Vinca minor* L., the solitary, lateral flowers are without the slightest evidence of subtending bracts. The different condition of the closely related periwinkle, *Lochnera rosea* (L.) Rchb., will be discussed presently.

Closely correlated with the predominance of cymose inflorescence in the family Apocynaceae is the occurrence with but few exceptions of decussate phyllotaxy. So much has been written concerning the spiral arrangement of appendages of the shoot as "primitive," a term of all too vague implications in many instances, that observations to the contrary might appear to have been suppressed by the sheer weight of consensus of opinion among morphologists. In the case of Apocynaceae, however, the reverse appears obvious.

Among the 132 genera recognized within the family by Schumann (1895) only twelve are characterized by spiral phyllotaxy. Of these, but one and two respectively are contained within the subfamilies Apocynoideae and Echitoideae, which have been found to have an elementary, or "primitive," carpological structure predominating (Woodson, 1930), while the alternate-leaved genera of Plumeroideae, characterized by the occurrence of generally more complicated, or "advanced," carpological conditions, number nine. Whorled phyllotaxy is found in fourteen genera of Plumeroideae and four of the Echitoideae enumerated by Schumann. In this connection it appears significant that of the eighteen genera with whorled phyllotaxy, no less than seven[1] are known to contain at least one species with normal, decussate foliage. In this, as in other

[1] *Aspidosperma, Condylocarpon, Couma, Gynopogon, Laubertia, Macrosiphonia, Pycnobothrya.*

families, there is an obvious correlation of whorled and opposite phyllotaxy indicating the derivation of the former from the latter, possibly by the aggregation of nodes.

Such deductions as the immediately preceding receive additional support by observations on the young seedlings of *Amsonia* spp.[1] and *Rhazya orientalis* (Dcne.) A. DC., the first stem-leaves of which are characteristically decussate. Two alternatives effect the adult, spiral phyllotaxy. In numerous instances among the seedlings under observation lateral buds were produced *in the axils of the cotyledons.* Upon subsequent development the arrangement of leaves upon such lateral branches was found in all cases to be normal for the adult condition of the species. The plumular shoot was short-lived. Somewhat less frequently among the seedlings a gradual change from decussate to spiral phyllotaxy was seen to occur upon the plumular shoot by the vertical translocation of nodes. The juvenile shoot was thereupon transformed directly to the adult condition. In innumerable instances more or less conspicuous vertical translocation of individual foliar nodes may be observed in species of Apocynaceae with normally opposite phyllotaxy.

Upon physiological-anatomical grounds opposite phyllotaxy and the occurrence of perfectly cymose inflorescence would appear to be unavoidably correlated. To many botanists the chief, if not the only, important characteristic of the cyme is the fact that for each axis a solitary, terminal flower exists which may be associated with a variable number of subsidiary floral members developing in basipetal succession. A most essential feature of the perfectly compounded cyme which has been overlooked generally, even by some students of inflorescence structure, is the almost geometrical precision which governs the expansion of its floral members. In such a simple dichasium of three flowers as has been described in a preceding paragraph, observable in innumerable genera of flowering plants in such families as Caryophyllaceae, Primulaceae, Gentianaceae, Apocynaceae, etc., the primary floral member termi-

[1] *A. Tabernaemontana* Walt., *A. brevifolia* A. Gray, *A. illustris* Woods., *A. pogonosepala* Woods.

nating the vegetative axis of stem or branch invariably blooms first. This is soon followed by the nearly simultaneous expansion of the two equivalent, lateral floral members immediately subtending.

If the dichasium be compounded to include for either branch a pair of lateral floral members subtending the secondary determinate pedicels, these will bloom shortly thereafter, in almost clock-like concert. This very impressive similarity of composition and unison of development of equivalent members of "perfect" cymes may appropriately be referred to collectively as its characteristic, or elemental "symmetry."[1] Common observation will probably lead one to object at this juncture that many, if not most, cymose inflorescences are not possessed of one or both of these "ideal" attributes under actual living conditions. Such is doubtless the case, and the remainder of this paper will be devoted to the occurrence of such irregularities among certain Apocynaceae and their possible evolutionary significance.

It is a fact quite easily observed that truly "perfect" cymes, whether di- or pleiochasia or derivatives of these, are found only upon flowering plants with opposite or whorled phyllotaxy. In no alternate-leaved species has this writer observed the strikingly symmetrical development of equivalent floral members so characteristic of the "perfect" (e. g. "ideal") cymes. The reason is doubtless anatomical and physiological: an inflorescence borne at the lower of two translocated nodes receives its vascular supply from the apical meristem somewhat earlier than the inflorescence immediately above. Hence subsequent development of the floral members is slightly in advance of that of the cyme immediately above, in spite of the fact that the two would be "equivalent" in the event of opposite phyllotaxy.

Although observations have been made over an unusually wide assortment of specimens during a number of years, as has been indicated in a preceding paragraph, the chief trends of

[1] This theory of the elementary symmetry of the ideal cyme will be found to place more emphasis upon the factor of time in development than the somewhat similar conception of "rhythm and symmetry" propounded by Goebel (1931).

the evolutionary development of the inflorescence in Apocynaceae may apparently be visualized from a review of a few characteristic representatives. In spite of the inevitable loss of minute detail, such an abbreviated account should possess a degree of clarity and simplicity difficult of attainment in a more extended, if more comprehensive account. It has been a matter of considerable disappointment that anatomical observations have been impossible because of the difficulty in securing fresh material of the critical genera. It is hoped that such data may eventually be secured to test the wholly gross morphological account which follows.

A final word of caution may be necessary to emphasize that perhaps no phase of the flowering plant's gross morphology is more variable than the inflorescence. The inflorescence is essentially a phase of branching of the shoot system, but it is vastly more complicated than vegetative branching, from which it has been derived. Hence the examples of inflorescence used to illustrate the observations which follow must be understood to represent *tendencies* perceived after wide study: they represent by no means the whole range of variation of a genus or species.

Explanation of Symbols Used in Diagrams.—In the diagrams illustrative of the succeeding paragraphs, dimensions have been maintained constant, despite disparities of the inflorescences in nature. The following symbols have been employed to denote floral members:

 — floral bud.

 — flower at anthesis or shortly thereafter.

 — fruit (in this and the preceding the relative size of symbols is indicative of the corresponding degree of development upon the actual specimen observed).

 — bract.

 — leaf.

 — undeveloped bud, floral or vegetative.

/ — broken portion of specimen.

 — whole mature inflorescence.

 — immature inflorescence.

The limitations of diagrammatic representation render impractical an attempt to indicate the decussate or spiral composition of the inflorescence. Branches, pedicels, and bracts which appear opposite and in the same plane must be interpreted as naturally decussate: similarly with the alternate members appearing as in the same plane which must be construed as naturally spiral.

Observations

Echites P. Br.

Our present knowledge of the genus *Echites (sensu stricto)* is limited to seven species and a putative variety which may be separated provisionally into four sectional groups centering about *E. tuxtlensis* Standl., *E. turbinata* Woods., *E. yucatanensis* Millsp., and *E. umbellata* Jacq., respectively. The aspect of the infloresecence of these species is reproduced in pls. 1–2. The best-known species of *Echites,* as well as the type of the genus, is *E. umbellata* Jacq., a liana occurring virtually throughout the Greater Antilles and extending to southern peninsular Florida, the Bahama Islands, and the coastal flats of northern Yucatan and British Honduras. The inflorescence of this species consists of one to several flowers, two, three, or four being the predominant numbers, borne in corymbose cymes. Tendencies of the inflorescence may be discussed briefly with the aid of five sketches provided in pl. 1.

The cymes of *E. umbellata* are predominantly alternate-lateral, but may be pseudoterminal as well. Such an individual is shown in pl. 1, fig. 5. In this case the axis is terminated by a

flower in full bloom. The two lateral branches bear one and two buds respectively, the solitary bud to the left being conspicuously larger than either of the two upon the opposite branch. The paired bracts of the branch to the right, in the axil of one of which the smaller lateral bud is found, indicate that the present condition was probably derived from a perfect cymule of three floral buds. Detection of a minute, abortive bud in the axil of such a superficially "empty" bract is usually possible upon careful dissection. At the base of solitary, lateral pedicels as that to the left of the figure are usually found a few rather indefinite, tiny bracts, also indicating that the uniflorous condition has probably been derived from a lateral cymule.

In fig. 2 of the same plate an inflorescence is shown in which the right lateral branch of the dichasium has failed to develop in the axil of its subtending bract which remains. The terminal flower is full blown. The left lateral branch consists of three well-developed, and one abortive, buds. The terminal bud of this cymule is about to expand, and is the largest of the three. The lateral bud to the left of the terminal is manifestly next in size, and is undoubtedly interpretable as the remnant of a reduced lateral cymule. The terminal bud of the right cymule is the smallest of the functional buds, and this fact appears to be correlated with the presence of the abortive, lateral bud at its base. Evidently the right cymule is slower to develop than the left because its axis has not been stripped of subsidiary axes dependent upon its vascular supply. At any rate, an examination of many specimens demonstrates an indubitable association of advanced development and potential blooming with increased reduction of the inflorescence.

Plate 1, fig. 1 illustrates a dichasium of three members, the terminal pedicel of which is bearing young fruit. The two lateral flowers are of approximately equal development. Two explanations of this cyme are possible: that the inflorescence as such is basic and elemental, or that the two lateral members have been reduced from pluriflorous, lateral cymules to the same degree, and thus expand with approximate simultaneity. Figure 4 represents a uniflorous condition of the inflorescence

of *E. umbellata*, not uncommonly found, in which, however, two abortive buds subtend. The truly uniflorous condition, without the presence of one or more abortive buds, has not yet been observed in this species.

In *E. crassipes* A. Rich., however, solitary flowers are borne, and with the aid of somewhat smaller foliage serve to distinguish this poorly understood endemic of Cuba. Even in the instance of this species, nevertheless, an indefinite and small number of minute bracts at the very base of the pedicel gives strong support to the assumption of reduction from a pluriflorous dichasium (pl. 1, fig. 3). The scope of variation in the relatively small inflorescence of *E. umbellata* increases with the number of specimens examined, and is plainly impossible to describe adequately at this time. An examination of even a few, however, is sufficient to form the opinion that the inflorescence of the species as a whole is undergoing reduction, and that the progressive reduction of a cymule tends to hasten the development of the remaining flower buds in relation to those of less reduced but equivalent cymules.

Plate 2 represents the inflorescence of four additional species of *Echites*. The group centering about *E. yucatanensis* is confined to Central America, and is most tangibly separated from the Antillean *E. umbellata* by the absence of the spiral contortion of the corolla-tube of the latter. Although the dichasium has advanced decidedly toward the umbellate condition, the general tendencies of the floral development of the former (pl. 2, fig. 3) are conspicuously similar to those of the latter species. In *E. turrigera*, known only from Guatemala, the inflorescence (pl. 2, fig. 4) is an almost typical, pluriflorous dichasium. Here also, however, the influence of unequal reduction of equivalent cymules in the disruption of the cymose symmetry is in unmistakable evidence.

Conspicuously smaller flowers set apart *E. tuxtlensis* and *E. turbinata* from the other species of *Echites*. Here also the inflorescence is noticeably more extensive. In the former (pl. 2, fig. 1) a cyme is found in which the primary branching is dichasial and the subsequent composition helicoid. From the previous observations upon *E. umbellata* one may be led to

infer that here, and perhaps in all such helicoid cymes, the single, outer flowers of the sympodium, blooming only slightly subsequent to the expansion of the median, or terminal flower, have been hastened in their relative development by their previous reduction from a pluriflorous cymule.

The inflorescence of *E. turbinata* (pl. 2, fig. 2) is of puzzling nature, the first branching being typically dichasial, but the ultimate branching apparently partaking of the nature of the aggregate dichasium, since each of the three members is subtended by one or two small, probably abortive, floral buds, or by paired bracts. A logical explanation is that in this species a simple dichasium is being derived from the extensive modification of a more complex system. As this species, which is an endemic of Costa Rica, is extremely rare in herbaria, it may be hoped that a fuller understanding of its inflorescence will result from increased collections.

Apocynum L.

Promising clues to the origin of the aggregate dichasium are found in *Apocynum,* a genus of few species remarkably widespread over temperate North America. In *A. cannabinum* L., a ubiquitous weed of fields and roadsides, the inflorescence is predominantly terminal and multiflorous, consisting of a much ramified aggregate dichasium (text-fig. 1, A). Accompanying the terminal inflorescence are always two subsidiary, lateral shoots, both of which may bear a varying number of foliar nodes, in which case both eventually terminate with an inflorescence similar to the first. In many instances only one of such branches produces foliage; in this case the other produces directly an inflorescence similar to the first, but usually somewhat smaller. Naturally this second lateral inflorescence comes to full development much sooner than the first because of the elimination of the intervening foliar nodes. In many instances both lateral shoots may produce inflorescences directly without the production of foliage, in which case they become an integral part of the terminal inflorescence.

Apocynum cannabinum is an obnoxious weed largely because of its size and long period of bloom. These attributes are the

result of its ability to produce inflorescences through a relatively long season by means of its dichotomous or cymose branching. A much less pestiferous weed is *A. androsaemi-*

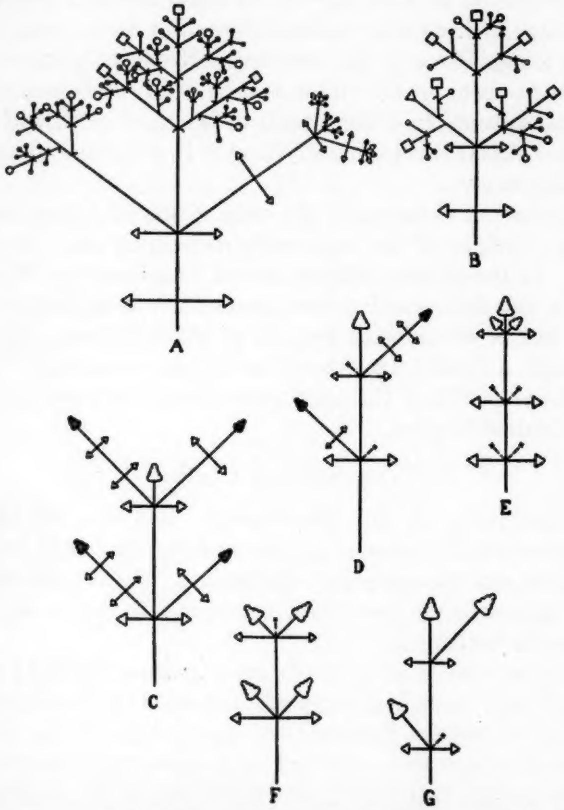

Fig. 1. Inflorescence structure: A—*Apocynum cannabinum* L.; B—*A. androsaemifolium* L.; C—*Forsteronia leptocarpa* (Hook. & Arn.) A.DC.; D—*F. paludosa* Woods.; E—*F. spicata* (Jacq.) G. F. W. Meyer; F—*F. amblybasis* Blake; G—*F. elachista* Blake. Explanation in the text.

folium (text-fig. 1, B), in which the lateral shoots accompanying the strictly terminal or median inflorescence do not tend to elongate as in the sister species. The blooming period, as well as the size of this species, is consequently relatively less.

"Aggregate dichasium" is evidently a well-chosen name for the inflorescence of *Apocynum*, from the phylogenetic standpoint; for if we read the data properly, it has been derived by the aggregation of a number of terminal dichasia through the elimination of the foliar nodes subtending them, hence the decussate composition of its branches. Recapitulatory evidence appears to occur in the inflorescence of *A. androsaemifolium* and other species, in which bracts of the median axis of the aggregate dichasium occasionally regain to a limited extent their foliar character.

Apocynum is apparently the only genus of Apocynaceae in which the origin of the aggregate dichasium may be read so easily. In the closely related genus *Trachomitum* Woods. of Eurasia, the inflorescence has become about as highly organized as in *Forsteronia*, an account of which follows. In *Poacynum* Baill., a close Asiatic relative of *Apocynum* and *Trachomitum*, the branches of the aggregate dichasium have undergone scorpioid modification.

Odontadenia Benth.

The evolution of the inflorescence of the echitoid genus *Odontadenia* would appear to approach the cincinnus from both the typical and the aggregate dichasium. Significant stages in this progression, drawn from representative species, are illustrated in text-fig. 2.

The inflorescence of *O. Hoffmannseggiana* (Steud.) Woods. is a variously modified, aggregate dichasium bearing few to relatively numerous flowers (text-fig. 2, A). In the specimen illustrated, which was collected by Tessmann in eastern Peru, two flowers are full-blown, one terminating the median axis, and one terminating the subsidiary axis to the right of the figure. It is clear that the floral bud terminating the equivalent, secondary axis to the left has failed to keep pace with the development of the sister determinate flower, and this fact is correlated with the fact that the cymule is composed of four flowering nodes and the one to the right of but two. It is significant also that the tertiary axes of the right cymule are in different stages of relative development: that to the left, consisting of

but one floral bud, is in a conspicuously more advanced stage than either of the three comprising that to the right. The same situation is found with respect to the two subsidiary cymules of

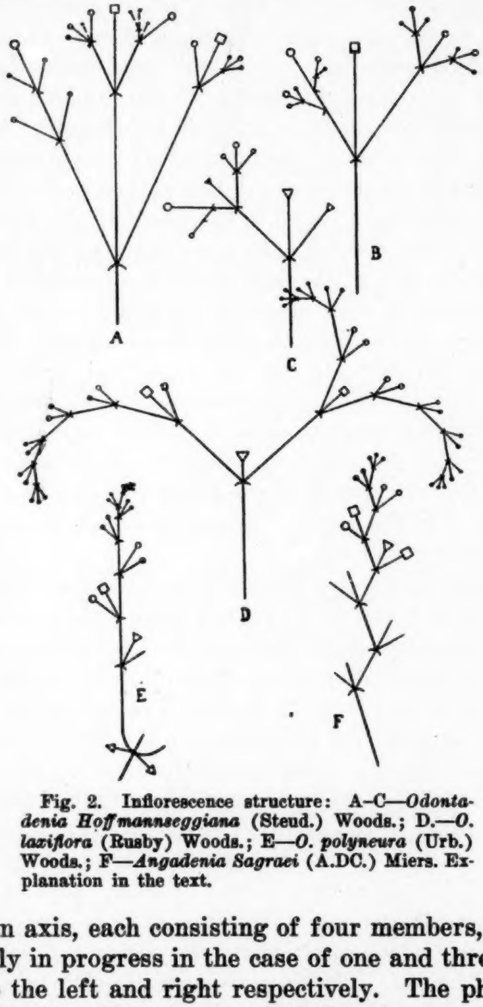

Fig. 2. Inflorescence structure: A–C—*Odontadenia Hoffmannseggiana* (Steud.) Woods.; D.—*O. laxiflora* (Rusby) Woods.; E—*O. polyneura* (Urb.) Woods.; F—*Angadenia Sagraei* (A.DC.) Miers. Explanation in the text.

the median axis, each consisting of four members, with abortion plainly in progress in the case of one and three of either cymule to the left and right respectively. The physiological result is clearly evident in the relatively advanced stage of development of the lone functional bud to the right.

The first stages of the development of a cincinnus are also observable in *O. Hoffmannseggiana.* In text-fig. 2, C, an instance is found in which the inflorescence consists of a primary, fruiting pedicel and two strongly unequal, secondary branches of one and six functional pedicels to right and left respectively. Although it happens that young fruit terminates both secondary axes of the dichasium, the size of the symbols is expressive of a significant disparity in relative development exactly like that found under similar circumstances in floral members.

An additional factor of great importance in the modification of the inflorescence is found in the effect of the vertical translocation of nodes. The translocation of the equivalent, tertiary cymules to the left of the inflorescence illustrated in text-fig. 2, B, shows that in such cases the members of the lower node are hastened appreciably in their development, even though those of the upper node may be somewhat more reduced in numbers. This fact, again, requires but an obvious anatomical-physiological explanation, since the lower node, differentiated first from the apical meristem, is effectively joined to the functioning conductive tissues of the shoot and root at a somewhat earlier time than the upper. Hastened development of its subtending members follows.

In *O. laxiflora* (Rusby) Woods. a peculiar modification of the inflorescence is found in which the main axis is regularly dichasial, but the secondary branch to the left has become helicoid by the repeated reduction of the right branch of each cymule to a solitary floral bud (text-fig. 2, D). The secondary branch to the right is compounded dichasially to the tertiary axes, which then become helicoid. The terminal flower of the secondary branch to the left naturally blooms before that of the branch to the right because of the greater degree of reduction of its axis.

The modification of the dichasium to a simple cincinnus is culminated in *O. polyneura* (Urb.) Woods. (text-fig. 2, E), in which a superficially indeterminate axis is compounded by paired pedicels borne in alternate succession subtended by one of a pair of bracts. The flowering axis is clearly a scorpioid sympodium, although it has lost the conspicuous zigzag aspect of less highly modified scorpioid inflorescences, as that of *Angadenia Sagraei* (A. DC.) Miers, illustrated in text-fig. 2, F.

Forsteronia G. F. W. Meyer

The inflorescence of *Forsteronia* has been described rather loosely as a panicle. A thorough study of representative species discloses the fact that a true panicle is absent in all. Various modifications of the thyrse are predominant, varying from typical, pyramidal outline to structures which superficially resemble the corymb and the spike, through the elongation or the virtual elimination respectively of the subsidiary axes. The recent discovery of a species with the structure of an almost typical, corymbose raceme heightens the significance of the inflorescence structure of this genus, and renders its study of great value in the evolutionary history of flowering axes generally. Text-fig. 3 provides diagrams of the inflorescence of various representatives of this genus.

The inflorescence of *Forsteronia* is composed of many flowers of relatively small size, rendering analysis and interpretation somewhat difficult. Relatively young inflorescences, frequently collected separately and preserved in small packets upon herbarium sheets, have been found extremely useful for study, since they may be boiled *in toto*, restoring a semblance of the living posture. After study such specimens may be partially dried and pressed between blotters, from whence they may be returned to the herbarium packets after complete desiccation. Such procedure serves to emphasize the convenient use of herbarium specimens for the study of gross morphology beyond the usual practice of taxonomic identification.

The elemental type of inflorescence in *Forsteronia* would appear to be the many-flowered, aggregate dichasium, such as that of *F. corymbosa* (Jacq.) G. F. W. Meyer, *F. floribunda* (Sw.) G. F. W. Meyer, and *F. portoricensis* Woods. In such an inflorescence (text-fig. 3, A), the terminal flowers of the median, as well as those of all secondary axes, bloom with approximate unison. It is possible that this rather arresting phenomenon may be in large part due to the successive reduction of the number of floral members borne upon the secondary axes from bottom to top, resulting in the pyramidal outline.

Focusing our attention upon the individual composition of the lateral members, it is found that the tertiary branches are

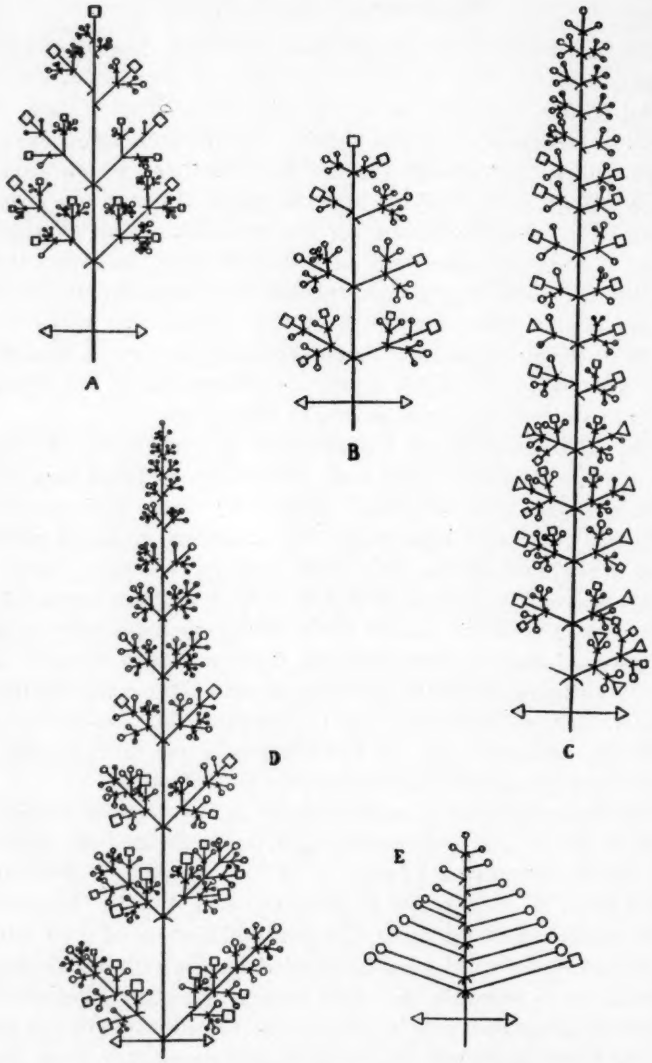

Fig. 3. Inflorescence structure: A—*Forsteronia corymbosa* (Jacq.) G. F. W. Meyer; B—*F. Velloziana* (A.DC.) Woods.; C—*F. thyrsoidea* (Vell.) Muell.-Arg.; D—*F. leptocarpa* (Hook. & Arn.) A.DC.; E—*F. simulans* Woods. Explanation in the text.

dichasial. The slight nodal translocation has apparently not succeeded in influencing effectively the phenology of the inflorescence.

The inflorescence of *F. Velloziana* (A. DC.) Woods. is a corymbose structure intermediate between the aggregate dichasium and the thyrse (text-fig. 3, B). In this inflorescence the symmetrical expansion of the terminal flowers of the secondary axes has been disrupted effectively by the reduction of certain branches, resulting in hastened development of certain of the floral members. The primary axis, however, is still determinate.

The first indications of the modification of the aggregate dichasium to the thyrse seen in *F. Velloziana* lead to the inflorescence type of *F. thyrsoidea* (Vell.) Muell.-Arg. (text-fig. 3, C), which is more or less typical of the thyrsiform structure, since the main axis is indeterminate with respect to the secondary axes, which still retain their dichasial composition variously modified. In this extensive inflorescence the small amount of variation in flower numbers among the secondary cymules from the first to the fifteenth pair of nodes can perhaps be explained by the assumption of reduction in number of floral members in basipetal succession. This assumption would also aid in explaining the acropetal development of the secondary cymules which is evident.

Typical panicles are apparently never found in Apocynaceae. The paniculate structure is closely approximated in the inflorescence of *F. leptocarpa* (Hook. & Arn.) A. DC., in which both the main and the secondary axes are indeterminate, although the tertiary and lesser branches remain determinate (text-fig. 3, D). The factors influencing the indeterminate modification of the primary axis of *F. thyrsoidea* may safely be supposed to have been identical with those effecting the indeterminacy of the secondary axes of *F. leptocarpa*.

Our knowledge of the evolution of the inflorescence in *Forsteronia* is culminated in *F. simulans* Woods., a rare liana of Colombia, in which the inflorescence is superficially a corymbose raceme with simple lateral pedicels. From the diagram of this "raceme" provided in text-fig. 3, E, however, have been

omitted numerous extremely inconspicuous bracts and abortive buds occurring rather irregularly upon the peduncle amongst the floriferous pedicels, which further exhibit a marked tendency of translocation. It appears obvious that this inflorescence has been derived from a thyrse characteristic of neighboring species.

One can scarcely fail to be impressed by the great range of modification of the inflorescence amongst species of *Forsteronia* which would appear to offer a most significant clue toward the solution of the questioned relationship of determinate and indeterminate inflorescences. The remaining known species of *Forsteronia,* numbering forty-one, present various gradients of the inflorescence structures of the five examples discussed in the preceding paragraphs. The great bulk of these show certain tendencies centering about the types represented by *F. Velloziana, F. thyrsoidea,* and *F. leptocarpa.* It is significant that although the inflorescence has not been employed to a great extent in the taxonomic separation of the species in a recent revision by this writer, additional morphological criteria used in speciation have resulted in a concurrent classification.

Species of *Forsteronia* show a progressive transformation of vegetative to floriferous axes, distinctly recalling that previously discussed in *Apocynum,* but in greater variety. In *F. leptocarpa* (text-fig. 1, C), the terminal, aggregate dichasium is regularly accompanied by two lateral, vegetative shoots which continue the extension of the massive liana characterized by this species. Each of such vegetative branches may be compounded similarly. A somewhat similar method of branching is found in *F. paludosa* Woods., in which, however, a single lateral branch is developed in alternate axils of the decussate leaves. An abortive, or dormant bud is regularly found in the axil of the opposite node, which can become stimulated to growth upon injury of the stem above its occurrence (text-fig. 1, D).

In *F. elachista* Blake a lateral inflorescence occurs with the strictly terminal, occupying the alternate axils of the foliar nodes as in the vegetative branches of *F. paludosa* (text-fig.

1, G). In the case of numerous tropical Apocynaceae, notably species of *Odontadenia*, an indefinite number of cataphylls are found occurring at the base of such lateral inflorescences. These are not observed subtending vegetative branches, or they are inconspicuous. A natural assumption which presents itself is that the alternate lateral inflorescences of *F. elachista* are homologous with the vegetative branches of *F. paludosa*. In *F. spicata* (Jacq.) G. F.W. Meyer (text-fig. 1, E), terminal inflorescences are accompanied by opposite lateral inflorescences. In *F. amblybasis* Blake the tip of the branches frequently appears to produce a dichotomous inflorescence of equal halves (text-fig. 1, F). This phenomenon is shown to have been produced by the non-development of a terminal floriferous axis, traces of which can frequently be observed. Normal opposite-lateral inflorescences also occur in this species.

Mandevilla Lindl.

The large genus *Mandevilla,* consisting of approximately 108 known species, is typified among the American representation of the subfamily Echitoideae largely by simple, racemose inflorescence. The mode of raceme is diverse both in number of floral members and gross construction, varying from rather lax corymbs to elongate spikes amongst neighboring species. Diagrams of the chief types of inflorescence are provided in text-fig. 4.

It would appear highly significant that *Mandevilla* and *Forsteronia,* in which the tendency from determinate to indeterminate inflorescence is clearly evident, are closely neighboring genera. The foliar glands of the majority of Forsteronias are of almost the same structure and occurrence as those of *Mandevilla* subgen. *Eumandevilla,* and the construction of the anthers of either genus is closely similar. An additional factor of great importance is found in the stigmata, or "clavuncles," which are massive and umbraculiform in all species of *Mandevilla,* and in all save one species of *Forsteronia* are fusiform to subcapitate. The exceptional species of the latter genus is *F. simulans* Woods., with an umbraculiform stigma which could

scarcely be distinguished from that of a Mandevilla. It will be recalled that the inflorescence of *F. simulans* further approaches that of *Mandevilla* in its virtually racemose character.

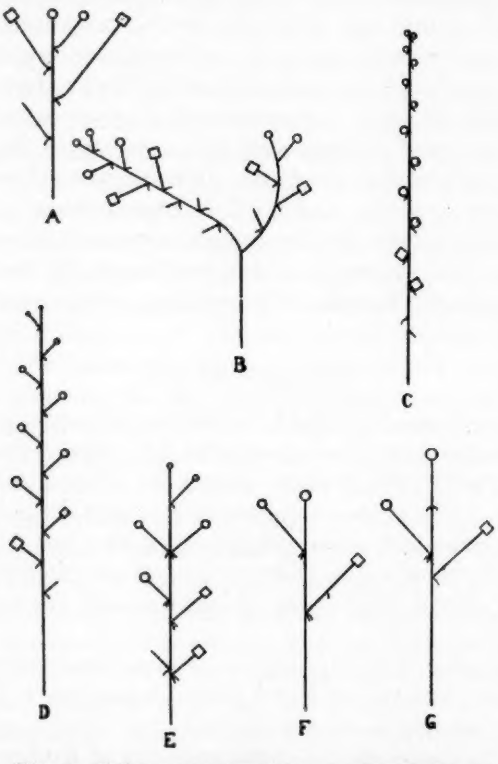

Fig. 4. Inflorescence structure: A—*Mandevilla callacatensis* Mgf.; B—*M. subpaniculata* Woods.; C—*M. scabra* (R. & S.) K.Sch.; D–G—*M. xanthostoma* (Stadelm.) Woods. Explanation in the text.

Although the inflorescence of the greatly preponderant number of Mandevillas may be characterized as simply racemose, a few, but highly significant exceptions occur. In *M. subpaniculata* Woods. (text-fig. 4, B), indubitable evidence of reduction from a compound inflorescence is found. That such composi-

tion is the effect of reduction, rather than of aggregation as was seen in *Apocynum,* for example, appears to be indicated in the fact that any such compounding is not in harmony with the vegetative symmetry of the shoot, but occurs somewhat irregularly, and often more obscurely than in the example figured. Less obvious clues leading to the conclusion of reduction are observable in the inflorescences of the closely related *M. Achrestogyne* Woods. and *M. bogotensis* (HBK.) Woods.

In *M. xanthostoma* (Stadelm.) Woods., an herbaceous and evidently a highly evolved member of this genus formerly included in the morphologically invalid genus *Dipladenia,* an interesting series of variations in inflorescence composition occurs which can scarcely be viewed other than as indicative of inflorescence phylogeny. A random collection of four such variations has been illustrated by diagrams in text-fig. 4, D–G, notes upon which follow:

1. Normal, or many-flowered, inflorescences of *M. xanthostoma* are of the typical, racemose type with alternate pedicels subtended by solitary bracts. Such inflorescences average roughly eleven to thirteen functional pedicels (text-fig. 4, D).

2. Abnormal, or relatively few-flowered, inflorescences tend toward a "pseudo-bostrychoid" racemose type with opposite pedicels, either or both subtended by more than one bract (text-fig. 4, E).

3. Multiplicity of bracts is frequently associated with opposite pedicels and reduced inflorescences, but not invariably (text-fig. 4, F).

4. The raceme may terminate indeterminately as well as pseudo-determinately by a terminal flower expanding slightly before the bud immediately below (text-fig. 4, G).

The unusual tendencies of inflorescence structure in such species as *M. subpaniculata* and *M. xanthostoma,* differing widely in their immediate intergeneric affinities, can easily be interpreted as indicating the evolution of the simple raceme characteristic of the genus as a whole from a primitive compound type similar to the thyrse. This evidence is entirely congruous with that found in the closely neighboring genus *Forsteronia.*

In this connection, the need of an anatomical investigation of those inflorescences, superficially racemose but with more than a single bract subtending each flowering pedicel, must be indicated. In the gentianaceous genus *Coutoubea*, it has been found that the inflorescence, described by systematists as a raceme, differs from a true raceme in the subtension of each flower by three to four inconspicuous decussate bracts. Recent investigation (Woodson, 1933) has disclosed the occurrence of occasional, abortive or dormant buds in the axils of these bracts which are detectable only in microscopic preparations. The "pedicels" of this inflorescence, therefore, are anatomically determinate axes, and the "raceme" itself could more accurately be described as a greatly reduced thyrse.

Corymbose and spiciform modifications of the raceme in *Mandevilla* are illustrated by *M. callacatensis* Mgf. and *M. scabra* (R. & S.) K. Sch. respectively (text-fig. 4, A–C).

Temnadenia Miers

The dichotomous cincinnus is a type of inflorescence characteristic of a number of apocynaceous genera, in which the flowering axis consists of a more or less elongate, naked peduncle terminated by two bracts of various size and texture subtending roughly equal, scorpioid branches. Noting the abscence of any interpretable structure in the crotch of the two frequently divaricate branches, one might be tempted to suppose the agency of dichotomy of the young growing initials of the inflorescence in early stages of development. Such superficially "dichotomous" inflorescences as those of *Temnadenia stellaris* (Lindl.) Miers (text-fig. 5, D) may occasionally be found to produce determinate flowers in the crotch of the scorpioid branches (text-fig. 5, E), however.

The suspicion that the inflorescence of *Temnadenia* has arisen from the elimination of the determinate flower of a continuous dichasium is heightened by an examination of the inflorescence of *T. stenantha* Woods. (text-fig. 5, F), recently discovered in northern Colombia, in which some of the uppermost branches may be clearly dichasial, with pedicels and bracts regularly disposed, although with unmistakable ten-

dencies toward the cincinnus. The lower branches of this inflorescence are of the superficially dichotomous development, even to the disappearance of the subtending bracts at the dichotomy.

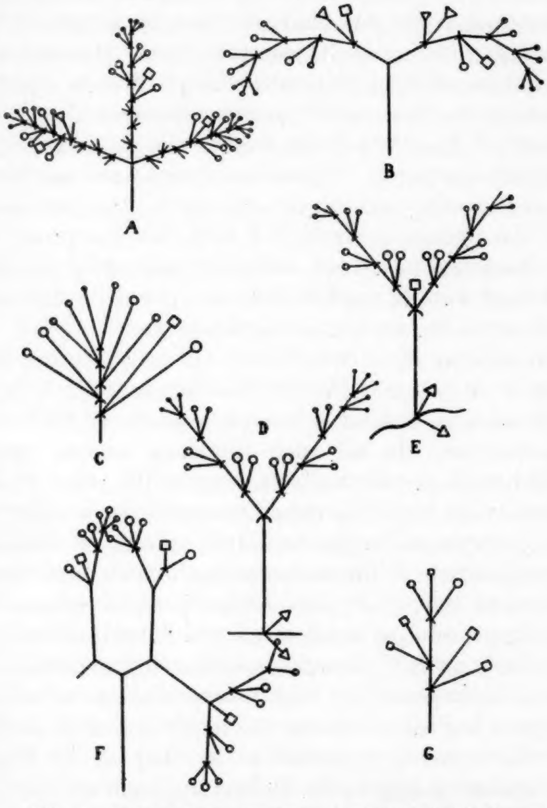

Fig. 5. Inflorescence structure: A—*Prestonia Meg'agros* (Vell.) Woods.; B—*P. portobellensis* (Beurl.) Woods.; C—*P. mexicana* A.DC.; D–E—*Temnadenia stellaris* (Lindl.) Miers; F—*T. stenantha* Woods.; G—*T. violacea* (Vell.) Miers. Explanation in the text.

The inflorescence of *T. violacea* (Vell.) Miers is usually simple and scorpioid (text-fig. 5, G), although individuals are not difficult to find in which derivation from such a floral axis

as that of *T. stellaris* is indicated by an inconspicuous subsidiary axis.

PRESTONIA R. BR.

The genus *Prestonia*, consisting of approximately fifty-four known species, is largely characterized by a type of inflorescence rather puzzling in its complications. In such inflorescences as those of *P. agglutinata* (Jacq.) Woods. (pl. 3, fig. 1) of the section *Coalitae*, and *P. quinquangularis* (Jacq.) Spreng. of the section *Acutifoliae*, the axis is simple and the pedicels scorpioidally arranged. These two species are selected for illustration since they exhibit to some extent the peculiar zigzag habit of the peduncle correlated with the scorpioid inflorescence of *Angadenia Sagraei*, evidently caused by the alternate left- and right-handed modification of a primitive dichasium, to which reference has been made previously.

Such species as *P. portobellensis* (Beurl.) Woods. (text-fig. 5, B) and *P. Meg'agros* (Vell.) Woods. (text-fig. 5, A) of the section *Annulares* exhibit a conspicuous di- or trichotomy of the inflorescence. In all such instances among species of *Prestonia* bracts are virtually lacking at the place of division of the floriferous from the naked branches, by which they lose the clue to a cymose origin found in species of *Temnadenia*. There appears to be little reason to doubt such dichotomous inflorescences as that of *P. portobellensis* to have been derived from the suppression of the determinate floral member and subtending bracts as in *Temnadenia*, indicating evolution from a continuous dichasium. If that interpretation be allowed, it would appear logical to assume the modification of the trichotomous inflorescences, represented by that of *P. Meg'agros* from an ancestral aggregate dichasium, such as that of *Forsteronia* species.

The section *Tomentosae* of *Prestonia* includes numerous species varying widely in their habit of inflorescence from simple to di- or trichotomous cincinni. In general, however, the tendency of inflorescence of these species is toward the condensation of the peduncle, producing such virtual umbels or corymbs as those of *P. mexicana* A. DC. (text-fig. 5, C, in which the pe-

duncle has been unnaturally extended to clarify its composition) and *P. brachypoda* Blake. The umbellate condition is closely approached amongst the species of *Thenardia* as well, in which the floriferous branches of a condensed, aggregate dichasium as that of *T. floribunda* HBK. (pl. 3, fig. 4) become successively foreshortened until the relatively elongate pedicels have the appearance of springing from a common receptacle subtended by numerous, involucre-like bracts as in *T. Galeottiana* Baill. The remarkable umbellate cymes of the genus *Malouetia* (cf. *M. Schomburgki* Muell.-Arg., pl. 3, fig. 2) have presumably had a similar origin.

Macrosiphonia Muell.-Arg.

Reduction from a pluriflorous condition has evidently resulted in the solitary, terminal flowers characteristic of the familiar North American species of *Macrosiphonia.* Since the evidence of reduction (i. e., position and composition of bracts and frequency of occasional lateral flowers) is used taxonomically in the delimitation of species, each will be discussed briefly.

Macrosiphonia hypoleuca (Benth.) Muell.-Arg., a low, suffrutescent species of the north-central Mexican plateau, is partially characterized by the terminal inflorescence consisting usually of a large, white, vespertine flower borne upon a relatively short pedicel subtended by two rather inconspicuous, paired bracts. Below the bracts is a peduncle ordinarily of about the length of the pedicel (text-fig. 6, A). The presence of the bracts reveals the compound nature of this superficially simple inflorescence, and their paired disposition would lead us to infer modification from a primitive cyme of which the present solitary flower might logically be viewed as the surviving determinate member.

Happily for this view specimens are not rare in which a second flower is found accompanying the determinate flower, obviously in the axil of one of the subtending bracts. An occurrence much less common is the formation of a complete three-flowered cymule (text-fig. 6, B). In at least one instance, however, a specimen from southern Mexico has been found in

which the appearance of a three-flowered raceme has been produced, presumably by the translocation of the normally opposite nodes.

Macrosiphonia Macrosiphon (Torr.) Heller differs from *M. hypoleuca* largely in the conspicuously foliaceous calyx-lobes, more or less petalaceous in the latter, and the broader, nearly concolorous leaves, which are conspicuously paler beneath in *M. hypoleuca*. The inflorescence of *M. Macrosiphon* also differs radically from that of its neighboring species, in the preponderant number of specimens examined, by the pedicel of the terminal flower becoming virtually sessile through the re-

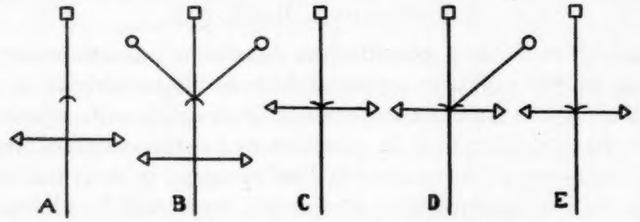

Fig. 6. Inflorescence structure: A–B—*Macrosiphonia hypoleuca* (Benth.) Muell.-Arg.; C—*M. Macrosiphon* (Torr.) Heller; D–E—*M. Brachysiphon* (Torr.) A. Gray. Explanation in the text.

duction of the peduncle (text-fig. 6, C). The primitively compound inflorescence is scarcely recalled save by the subtending, paired bracts which remain. These also may virtually disappear. No instances have been observed in which floral members have been formed in the axils of the bracts. The appearance of a perfectly simple, terminal flower in this species through reduction evidently depends upon the impending elimination of the already inconspicuous floral bracts. *Macrosiphonia Brachysiphon* (Torr.) A. Gray and *M. Hesperia* I. M. Johnston have been collected with both one and two flowers constituting the inflorescence (cf. *M. Brachysiphon*, text-fig. 6, D–E), which is practically devoid of a peduncle in either.

The opinion has been expressed elsewhere (Woodson, 1930) that the North and South American species of *Macrosiphonia* may have had independent derivation from some common stock such as that of the large and widespread genus *Mandevilla* or

its primitive progenitor. This conjecture receives support in the structure of the inflorescence of either group. That of South American species may be composed of either few or solitary flowers, which is somewhat less common. When few flowers occur, as in *M. longiflora* (Desf.) Muell.-Arg. (pl. 3, fig. 5), they appear in racemose disposition. Immediately subtending the calyx-lobes, however, is always observable a cluster of bracts which would indicate derivation from such a compound floral axis as that of the thyrse, for example. It has been pointed out previously that the mode of inflorescence in *Mandevilla* may be supposed to have been derived from a thyrse.

Additional instances in which a multiplicity of bracts supposedly remnant from a pluriflorous inflorescence is observable directly subtending a solitary flower borne in a lateral position are illustrated by *Elytropus chilensis* (A. DC.) Muell.-Arg. and *Macropharynx spectabilis* (Stadelm.) Woods. Specimens of either have been found in which one or two supernumerary floral members have been developed.

Vinca L. and Lochnera Rchb.

Vinca minor L. and *Lochnera rosea* (L.) Rchb. are among the most familiar garden plants. The former, popularly known as "running myrtle," is supposedly indigenous to the northern Mediterranean area, but has been so widely and so easily cultivated that it has become naturalized over a large part of western Europe and temperate North America. The latter, known as "periwinkle," has so successfully colonized the tropics of both hemispheres that considerable doubt surrounds the whereabouts of its original home, although it is probably from the Old World, the provenience of the two remaining species of the genus. A tender, ever-blooming annual, it forms an almost indispensable bedding plant in parks of the United States.

The inflorescence of *V. minor* (text-fig. 7, C) consists of solitary, lateral flowers. It is interesting to note, further, that the flowers appear only upon the semi-erect shoots produced in the early spring and summer from the creeping, perennial stolons. Not all the leaves of such shoots subtend flowers. The flowers

of *L. rosea* are produced regularly in lateral pairs subtended by the foliage leaves (text-fig. 7, A). The pedicels are arranged radially with respect to the stem axis and the subtending leaf; and the central flower always expands first. As the leaves are decussate, pairs of flowers are in nearly all cases found in the axil of only one of the paired leaves, ascending the axis spirally. It is clear that the axis of the inflorescence of *L. rosea* is a sympodium derived from a cincinnus.

Among many flowering individuals of *L. rosea* occasional abnormalities are found in which only a single flower is formed in the axil of a subtending leaf (text-fig. 7, B). Considering the very close relationship of the genera *Vinca* and *Lochnera,* it

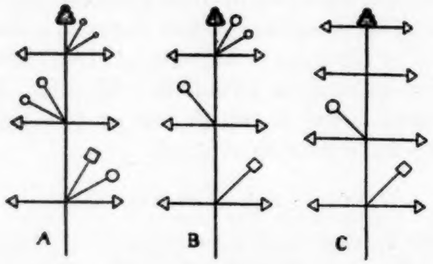

Fig. 7. Inflorescence structure: A–B—*Lochnera rosea* (L.) Rchb.; C—*Vinca minor* L.

seems more than likely that the indeterminate flowering axis of the former, bearing solitary, lateral flowers in spiral fashion, should represent derivation from such a sympodial axis as that of the latter.

Discussion

The necessity of a general review of literature concerning the inflorescence is obviated by the very full historical account given by Parkin (1914), whose admirable treatment of the evolution of the inflorescence remains our most comprehensive. In view of the great importance of that memoir and of the somewhat different conclusions to which the present writer has arrived, it would doubtless be both appropriate and serviceable to combine a discussion of the apparent evolution of the inflorescence in Apocynaceae with a rather extended criticism

of the views so ably expressed by Parkin. In introduction, it is scarcely possible to recall too forcefully that this writer's opinions are based upon observations within a wide range of a single family. Although intensive study within a single natural group, even though large, entails indubitable benefits, it can scarcely be said to result in conclusions which are applicable to all groups equally. This will become apparent in a subsequent paragraph. On the other hand, it rarely happens that a general biological principle, such as that influencing the modification of the inflorescence, can be true of a single natural group, and of none of its closely neighboring relatives.

In his study of the inflorescence herbarium specimens were virtually ignored by Parkin upon the assumption of imperfect evidence offered by them. However, recourse was had to a large number of living plants selected from species commonly cultivated in English gardens. Special emphasis was placed in this selection upon dicotyledonous representatives of the so-called "primitive alliances," such as Magnoliales, Ranales, Papaverales, etc. Evidently inspired by the frequent occurrence of solitary, terminal flowers in plants belonging to such orders of established antiquity, Parkin was led to conclude that in the primitive inflorescence "flowers were originally borne in a solitary fashion, and that the clustering of them together without intervening foliage is a later development." Upon this assumption, he quoted the familiar Euclidean "reductio ad absurdum" to dispel Church's interpretation of the solitary flower of *Pyrus Cydonia* as a reduction from the many-flowered inflorescences of such species as *P. Aucuparia* (Church, 1908).

Parkin's statement that the solitary, terminal flower is an ancient structure approaches the platitudinous when one reflects that the flower itself may be defined as a highly specialized, contracted short shoot bearing a collection of sporophylls with or without an accompanying envelope. Quite likely, through past ages isolated progenitors of the modern Angiospermous flower, occurring terminally and isolated by intervening foliage, became aggregated to form a specialized branch system coincident with the evolution of the flower itself. But to trace the very foundations of the evolutionary development

of the inflorescence among the extant Angiospermae is a dangerous undertaking none the less. No doubt the floral organization of the Ranunculaceae may be considered as "primitive" from several points of view, but few would extend that interpretation to the herbaceous habit so conspicuously predominant in the family. Similarly, although *Papaver* is clearly a genus of great antiquity, we would be slow to describe its gynoecium as "primitive" or elemental. It should clearly be recognized that groups of plants may possess palingenetic and cenogenetic characters side by side; our recognition of the former should not confuse our interpretation of the latter, although not to do so is manifestly difficult at times.

In supporting his contention of the primitive nature of the solitary, terminal flower among Angiosperms, Parkin cited the existence of terminal strobili in the Bennettitalean-Cycadalean plexus, now generally assumed to represent a primordium from which the flowering plants may have evolved. He noted, however, that the solitary, terminal strobili of the Cycads are occasionally accompanied by supernumerary members at the stem apex. The continuation of the vegetative growth is accomplished by a lateral bud, and a sympodium results. The anatomy of the axis of Cycads discloses the existence of a telescoped[1] sympodium essentially cymose in its composition, as Miss Smith (1907) has pointed out. In the Bennettitales, also, the branching of the Triassic *Williamsonia (Anomozamites) angustifolia* (Nathorst, 1902) and the Jurassic *Wielandiella* is of the sympodial type. The branching axis of the former, consisting of a system of relatively slender stems terminating in a strobilus surrounded by a rosette of leaves below which two equal branches are found similarly compounded, bears an unmistakable similarity to the modern dichasium of Angio-

[1] Apparently A. P. De Candolle (1827) was the first to use the metaphor of the telescope in describing extension and condensation of axes: "Je me ferais peut-être comprendre plus complètement par une métaphore bien grossière: supposons une branche florale organisée comme une lunette d'approche, qui porterait un pédicelle au haut de chacun des tubes qui la composent: que tous les tubes soient déboîtés et alongés, vous aurez une grappe; repoussez ces tubes à moitié, ce sera encore une grappe, mais très-courte; rentrez-les complètement, et vous aurez une ombelle terminale.

sperms, and the resemblance would appear to be more than fortuitous. It would appear a fruitless task to search for the earliest indications of the inflorescence among the extant flowering plants: the origin of the inflorescence is at least as remote as the origin of the flower, and a greater antiquity seems probable from the evidence of paleobotany.

Development of the pluriflorous inflorescence from the solitary, terminal flower is accomplished according to Parkin by the appearance of subordinate, lateral flowers literally "pushed out" of the axils of the subtending leaves of the original, terminal floral member. The continual "emitting" of subordinate flowers forms the first type of compound inflorescence: the dichasium. This process is illustrated in the genus *Papaver* by such species as *P. Rhoeas, P. strictum,* and *P. pilosum* in a series of floral accumulation, as we might express it for want of a better term.

The naivety of this conception of floral "emission" is heightened by the causal agent, ascribed by Parkin (1914) with some qualification to "a superabundance of reproductive material, more than the shoot could utilize in the formation of a single flower." This somewhat feeble effort to drag the continuity of the germ-plasm into the discussion of the inflorescence serves to illustrate rather indirectly the perplexing fact that although much is known concerning the "geometry" of plants, little indeed is understood of the causal mechanism responsible for it. Our easiest task, consequently, is to express structural modifications of plants in terms of the geometrical pattern approaching more nearly universal application throughout specific, natural groups. One might cite the example of dichasial branching, which is infinite in its theoretical extension. Practically, however, certain internal and external factors limit the expression of the dichasium to a definite numerical range of floral members in one species, and to a slightly different range in another.

In the end, the morphologist finds in nearly any highly developed group a "reduction series" in evolutionary history much easier to read than an "ascending series." Time and again the morphologist has found himself deceived by the ap-

parent "simplicity" of species and genera which have suffered reduction from the more elaborate geometrical pattern of their relatives during the inscrutable course of evolution. It should not be necessary to recall that our modern flowering plants represent a very ancient and specialized development whose foundations are still, and possibly always will be, exasperatingly obscure. The so-called "primitive alliances" are evidently scarcely more ancient, from available paleobotanical records, than others from which they have been separated by the imposition of an imperfect system of classification. The herbaceous habit of such genera as *Papaver,* for example, might be cited as but one evidence of a long and specialized evolutionary development.

From the evidence briefly reviewed for *Echites umbellata,* the evolution of the uniflorous condition from pluriflory through the agency of reduction appears plausible, for we have the evidence of reduction at hand in the form of "empty" bracts and occasional abortive buds. The opposite assumption, which would logically include the inference that such buds are in a nascent stage, would appear preposterous. This writer finds ample sympathy for the independent and earlier views of Church (1908) respecting the evolution of the inflorescence in *Pyrus* to which reference has been made in a preceding paragraph.

The result of reduction upon the development of the remaining floral members of the inflorescence described in the previous paragraph is strikingly similar to that of the old horticultural practice of "picking out the suckers," or "disbudding," in the cultivation of tomatoes, grapes, and other cultivated plants, by which the growers seek to influence the subsequent development of the remaining members. "Disbudding" is also practiced in the forcing of cultivated chrysanthemums, etc., and the time of blooming can be controlled largely through this agency. Gardeners using the same method in the cultivation of such plants as *Paeonia* have observed that plants which "disbud themselves," e. g., by natural abortion of floral buds, bloom earlier and have larger flowers than those whose full floral complement develops unchecked.

Much the same effect can be produced experimentally by amputating floral buds of such an inflorescence as the multiflorous thyrse of the apocynaceous *Amsonia Tabernaemontana* Walt. Precaution must be taken, however, to arrest the development of the buds at a sufficiently early stage and with the slightest possible injury. All experiments made in this manner have not been wholly satisfactory, due probably at least in part to the latter factor. Since it is impossible wholly to exclude the factor of injury, even slight success in modifying the symmetry of the cyme may be regarded as significant, the more subtle influence of natural abortion being beyond perfect imitation.

Concerning the transition of the indeterminate from the determinate inflorescence, Parkin (1914) envisions a process in which "the number of lateral floral shoots increase, so that the main terminal flower no longer blooms first. The flowers then tend to open in acropetal succession from the commencement. The next step comes about through the flower-buds of the uppermost part of the inflorescence never expanding; this part, in fact, becomes arrested in its development and finally aborts, leaving a mere filament or protuberance in its place. In this way the original terminal flower disappears. The inflorescence is now racemose." In the light of what the author has said as previously reported concerning the supposed primitive, few-flowered inflorescence, one can scarcely avoid confusion in attempting to harmonize this last statement with the innumerable-flowered cymes of *Statice* and the relatively few-flowered racemes of *Plumbago* among Plumbaginaceae, to cite only one example. From Parkin's statement one would be justified in expecting racemes to contain more numerous flowers than cymes. Such is scarcely the case. The flexibility of the extent of the cyme might be likened in potentiality to that of the compound interest table.

On the other hand, failure of the apex of the peduncle to produce a terminal flower is not an inalienable characteristic of the raceme. In racemes of but few flowers a terminal member frequently occurs. This has already been demonstrated for the genus *Mandevilla* of the Apocynaceae (cf. text-fig. 4, A–G).

In perhaps no other particular are the observations of Parkin and those of this writer in greater contrast than in the immediate agency involved in the transformation of the indeterminate from the determinate mode of inflorescence. Both views are based upon anatomical-physiological assumptions. The view of Parkin may be epitomized in the statement that as the lower floral members increase in number, the development of the apical members is hindered by the increasing demands upon the conductive facilities of the axis, supposedly. In the preceding observations among the Apocynaceae, on the other hand, a totally different process is adduced. It has been found in *Echites* that in the instance of two equivalent cymules of identical composition the *reduction* of one or more floral members of one will hasten the development of the other component members, thus effectively disrupting the characteristic "symmetry" of the two equivalent cymules. It has been inferred with ample evidence that the cincinnus and the bostryx have evolved from the dichasium in this family through the reduction of a whole cymule to a solitary flower, thus invariably hastening its development second only to the primary determinate flower with which it becomes associated.

It is understood that reduction has effected *one* of the lateral cymules of a continuous dichasium to the production of the cincinnus or the bostryx. The effect of the reduction of *both* lateral cymules of an aggregate dichasium may be computed artificially: its demonstration in nature is afforded in the large genus *Forsteronia,* by which it has been shown that closely related species intergrade from aggregate dichasial inflorescences to a raceme through various modifications of the thyrse.

Having traced the development of the more important types of determinate and indeterminate inflorescences amongst the Apocynaceae, it becomes easy to extend our understanding; by the reduction of the pedicel to derive the spike from the raceme, and by the reduction of the peduncle and the compensating elongation of the pedicel to produce the corymb and the umbel, which may evidently be derived from both determinate and indeterminate forebears. Although generalizations are fre-

quently weak in the face of detailed attack, it may be permitted to visualize the writer's conception of the evolution of the fundamental types of inflorescence in Apocynaceae as represented in text-fig. 8.

At this juncture prominence should be given to the fact that reduction of floral members does not always hasten the de-

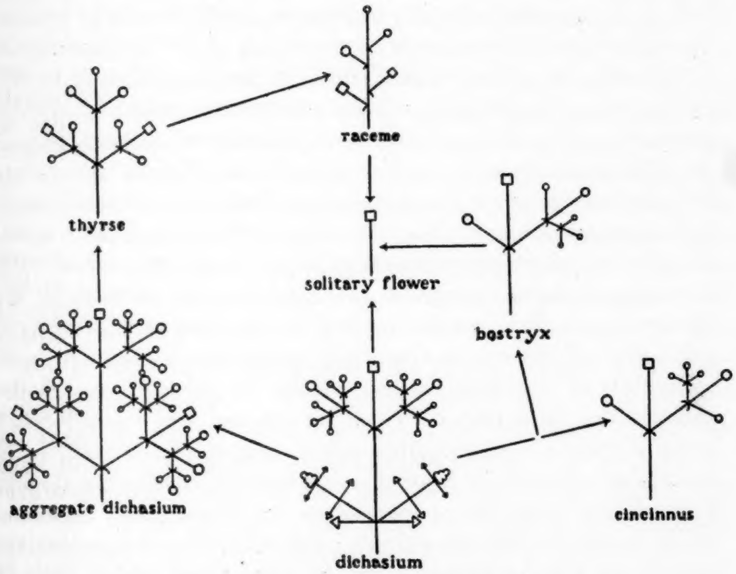

Fig. 8. Schematic diagram of the supposed relationship of certain types of inflorescence in Apocynaceae. Explanation in the text.

velopment of the remaining members of a cyme. Early in the course of these investigations recourse was had to members of other families to ascertain whether the same procedure is common. Selecting families containing familiar representatives bearing cymose inflorescences, it was soon found that the same principles discovered in Apocynaceae are apparently applicable in members of such families as Ranunculaceae, Rosaceae, Primulaceae, Gentianaceae, etc. In the family Caryophyllaceae, characterized by the predominance of the cyme, how-

ever, the principle of reduction in the disruption of cymose symmetry appears to be completely reversed. One needs but examine a colony of such a species as *Arenaria patula* to discover that the terminal flower of a somewhat reduced cymule actually blooms somewhat later than the terminal member of an equivalent, less-reduced branch. The reversal, moreover, appears widespread if not universal throughout the family, as well as in members of Convolvulaceae, and it would be odd indeed if it were unique among the flowering plants in this respect.

The solution of the enigma which is thus introduced, as well as the actual mechanism of the phenomena noted in Apocynaceae, etc., would appear to lie in a study of the anatomy of the inflorescence, a virtually untouched field since the rather few students of the inflorescence as a whole have limited themselves to gross morphology save in special instances. A decidedly hypothetical conception which must be tested by a future anatomical study of the inflorescence to explain the divergent results of reduction in Apocynaceae on the one hand and Caryophyllaceae on the other, might involve the divergent reduction of vascular tissues within the respective inflorescences: the reduction of vascular tissues and its attendant physiological effects possibly being limited to the pedicels of discarded members in Apocynaceae, thus redistributing the full flow of the conductive elements to the fewer floral members which would benefit accordingly; the reduction of vascular tissues in the Caryophyllaceae on the other hand taking place in the peduncular axes, thus hindering the development of the branch system as a whole. At any event, the primitive nature of the cyme in Caryophyllaceae should be established by future studies of the inflorescence of the group; here also, as in Apocynaceae, etc., the solitary flower is evidently a condition derived from pluriflory.

Minor points of criticism of Parkin's observations, in the light of the present writer's investigations on the inflorescence of Apocynaceae, may be dismissed without discussion. It should be noted that both are in agreement concerning the primitive nature of determinate and the derived condition of

indeterminate inflorescences. It is suspected that Parkin's inferences concerning the method by which the indeterminate mode was derived from the determinate were unfortunately affected by the fact that his illustrations include no perfectly symmetrical representatives of the latter. It is easily appreciated that the most characteristic features of the dichasium, for example, are lost in species with alternate, or spiral phyllotaxy, as has been indicated in an earlier section of this paper.

Summary

The following conclusions have resulted from a study of the inflorescence structure of numerous representatives of Apocynaceae throughout the distribution of the family, as revealed by both living and herbarium specimens. Special emphasis has been placed upon the American representatives of the subfamily Echitoideae, an evidently natural group lately studied by this writer (Woodson, 1933) from the combined aspects of floral anatomy and taxonomy.

1. The dichasial cyme appears to be the primitive inflorescence of the family.

2. The symmetry characteristic of the composition and sequence of development of equivalent cymules of the inflorescence of *Echites umbellata* Jacq. is found to be profoundly modified by unequal reduction of the component floral members. Reduction of one or more lateral members of a cyme is found to accompany a somewhat hastened development of the remaining members. This effect of reduction appears constant, or relatively so, amongst Apocynaceae and certain other families, but appears to be reversed in Caryophyllaceae (and Convolvulaceae) for reasons which are briefly conjectured. Such an agency is found to parallel long-established horticultural practices, such as "picking out the suckers," and "disbudding."

3. Reduction of a single branch of a continuous dichasium always to the right or left of the determinate flower, or to the right and left alternately, results in the production of a bostryx or a cincinnus respectively.

4. The transformation of the inflorescence from an aggre-

gate dichasium to a raceme through various modifications of the thyrse is traced amongst the species of the genus *Forsteronia.* This progression has evidently been actuated by the progressive reduction in acropetal fashion of both the decussate pairs of branches of an aggregate dichasium.

5. The spike is derived from the raceme; the corymb and the umbel are derivative from both determinate and indeterminate inflorescences.

6. Solitary flowers, whether terminal or lateral, are apparently derived from a previous condition of pluriflory through the agency of reduction.

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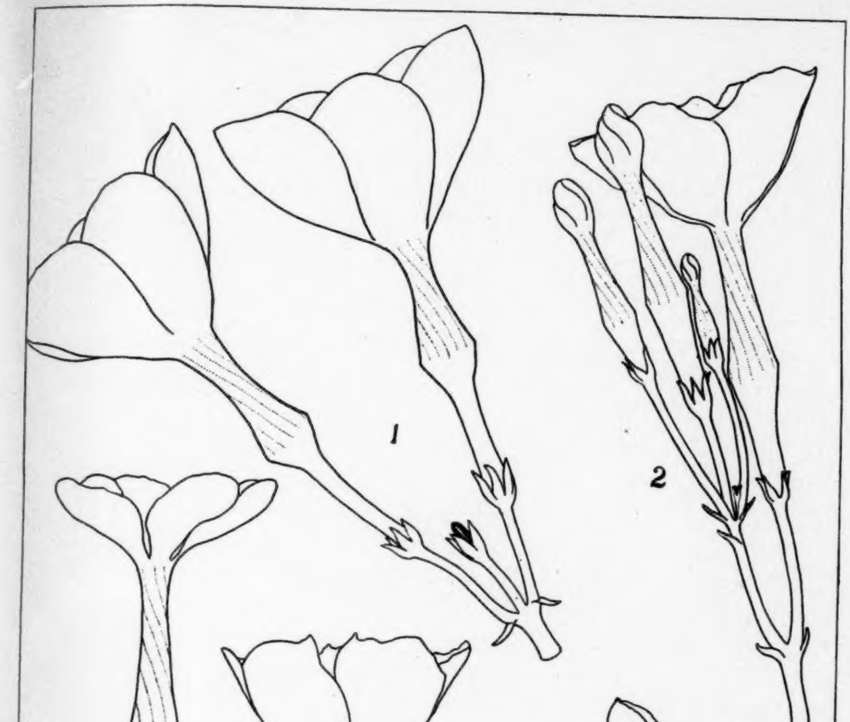
EXPLANATION OF PLATE

PLATE 1

Figs. 1-2, 4-5. Variation in inflorescence structure amongst individuals of *Echites umbellata* Jacq.

Fig. 3. Inflorescence structure of *E. crassipes* A. Rich.

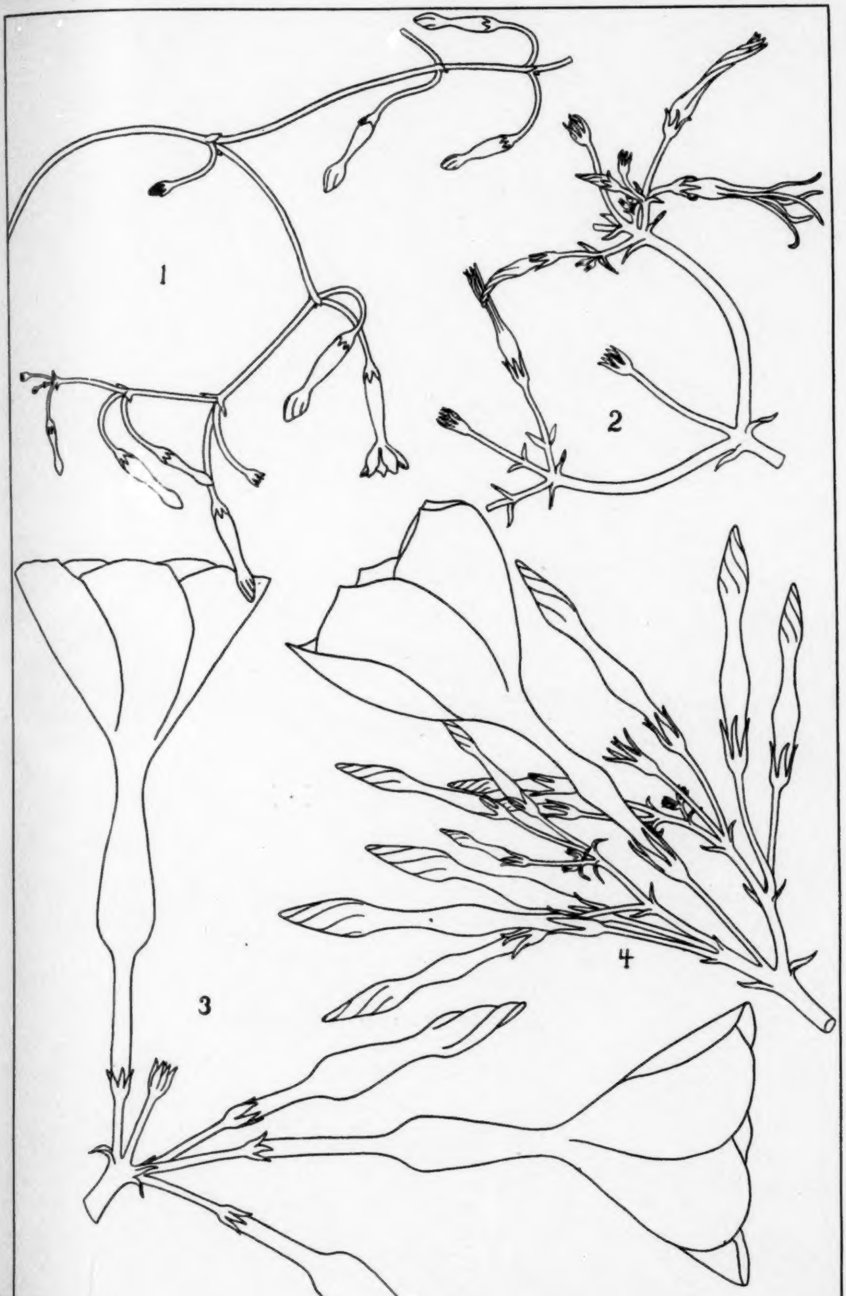


WOODSON—INFLORESCENCE OF APOCYNACEAE

Explanation of Plate

PLATE 2

Fig. 1. *Echites tuxtlensis* Standl.
Fig. 2. *E. turbinata* Woods.
Fig. 3. *E. yucatanensis* Millsp.
Fig. 4. *E. turrigera* Woods.



WOODSON—INFLORESCENCE OF APOCYNACEAE

Explanation of Plate

PLATE 3

Fig. 1. *Prestonia agglutinata* (Jacq.) Woods.
Fig. 2. *Malouetia Schomburgki* Muell.-Arg.
Fig. 3. *Fernaldia pandurata* (A.DC.) Woods.
Fig. 4. *Thenardia floribunda* HBK.
Fig. 5. *Macrosiphonia longiflora* (Desf.) Muell.-Arg.

WOODSON—INFLORESCENCE OF APOCYNACEAE

A NEW KALLSTROEMIA FROM TEXAS

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Kallstroemia hirsuta n. sp.[1] Ascending or erect annual, 1–2 dm. high; stems 1–several from the base, densely hirsute and strigose-pubescent, the hirsute hairs with pustulate bases; leaves 2–4.5 cm. long, oblong to ovate-oblong, petiolate, densely hirsute and strigose-pubescent on both surfaces, the petiole about as long as the lower pair of leaflets; leaflets 3–6 pairs, sessile, obliquely oblong or ovate, 7–14 mm. long, 3–8 mm. wide, obtuse or acute, about equal in size, the terminal more oblique; stipules lance-oblong, 3–4 mm. long, 1–1.5 mm. wide; calyx-lobes linear to linear-lanceolate, 10–13 mm. long, 1.5–2.5 mm. wide, hirsute and strigose-pubescent on the outer surface, the chartaceous margins inrolled in fruit; petals about 5, deltoid-ovate, 18–23 mm. long, probably white or yellowish, not marcescent; fruit compressed-oval in outline, 8–10 mm. wide, 5–6 mm. high, outer surface of carpels not tuberculate but the median portion and the two edges prominent and connected by transverse ridges, densely hirsute, particularly on the raised portions; persistent style or beak 8–10 mm. long, hirsute at the inconspicuously swollen base, stigmatic portion 1.5–2 mm. long, furcate.

TEXAS: Langtry, Valverde County, May, 1913, *C. R. Orcutt, 6126* (Mo. Bot. Gard. Herb.) TYPE.

This species is most closely allied to *K. grandiflora* Torr., from which it may be separated by the following characters: the entire plant is densely pubescent with hirsute and strigose

[1] **Kallstroemia hirsuta** sp. nov. Annua 1–2 dm. alta, dense hirsuta et strigoso-pubescente; foliis oblongis aut oblongo-ovatis utrinque pubescentibus; foliolis 3–6 paribus, sessilibus, 7–14 mm. longis, 3–8 mm. latis; stipulis lanceolato-oblongis, 3–4 mm. longis, 1–1.5 mm. latis; lobis calycis linearibus vel lineari-lanceolatis, 10–13 mm. longis, 1.5–2.5 mm. latis; petalis ca. 5, deltoideo-ovatis, 18–23 mm. longis; carpellis non tuberculatis parte medio et marginibus prominentibus; stylo 8–10 mm. longo, ad basem hirsuto.

Issued March 25, 1935.

hairs intermixed; the carpels are not tuberculate on the outer surface nor merely equally strigose but have the median portion and the outer edges raised and these connected with transverse ridges, and especially the raised portions hirsute with a small amount of strigose pubescence intermixed; beak hirsute at the base only instead of strigose nearly to the stigmatic portion.

Explanation of Plate

PLATE 4

Kallstroemia hirsuta Williams. From the type specimen, *Charles Russell Orcutt, 6126*, in the Missouri Botanical Garden Herbarium. ⅔ natural size.

WILLIAMS—KALLSTROEMIA HIRSUTA

A CRITICAL STUDY OF CERTAIN EPAPPOSE GENERA OF THE HELIANTHEAE-VERBESININAE OF THE NATURAL FAMILY COMPOSITAE[1]

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Introduction and Acknowledgments

This paper endeavors to present the results of a study of certain epappose genera of the tribe Heliantheae-Verbesininae of the natural family Compositae. The genera *Balsamorhiza, Zaluzania, Greenmaniella, Iostephane, Echinacea,* and *Ratibida* have been dealt with, first, with regards to their comparative morphology and probable phylogenetic relationships, and second, from a taxonomic point of view. The other genera which are occasionally referred to have been studied only for their phylogenetic and generic relationships. The more closely related of these genera, and especially the epappose ones, are included in the generic key.

The writer takes this opportunity to express his appreciation and gratitude to those who have made this work possible. Particularly is he under obligation to Dr. George T. Moore for the facilities of the herbarium and library of the Missouri Botanical Garden. Sincere appreciation is hereby expressed to the curators of the various herbaria from which specimens have been borrowed, thus making this study possible. He is also indebted to Miss Nell C. Horner, Librarian, for assistance in bibliographical matters. Especial gratitude is due Dr. J. M. Greenman, under whose direction and supervision this work has been carried out, for ready and helpful suggestions given throughout this study.

[1]An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

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PART I. GENERAL DISCUSSION

COMPARATIVE MORPHOLOGY

The genera previously mentioned, as well as *Dracopis* and *Rudbeckia,* will be here contrasted and compared. The chief distinctions are found in the involucre, the receptacle and pales, the corollas, and the achenes. The achenes and corollas present the characters of major importance in the generic differentiation.

Involucre.—The involucres of the genera studied are so uniform that it would be rather difficult to recognize any one of these genera on this character alone. The variations, however, do fall into five distinct categories: (1) the *Ratibida-Dracopis* type; (2) the *Rudbeckia-Echinacea* type; (3) the *Balsamorhiza-Iostephane* type; (4) the *Zaluzania* type; and (5) the *Greenmaniella* type.

The bracts of the involucre of *Ratibida* and *Dracopis* are so similar that it would be impossible to separate them on form alone. They are biseriate, the outer series linear, reflexed or spreading, herbaceous, and two to three times longer than the inner. Those of the inner series are about as long as the pales, but they are more herbaceous in texture, have acute apices, and a plane surface. The pales are conduplicate and marked by a brownish resin duct along each margin. The character of the involucre would be sufficient to separate these genera from those that follow.

The *Rudbeckia-Echinacea* type of involucre is of little importance in generic differentiation. The bracts are two- to three-seriate, herbaceous, linear to linear-lanceolate, and more or less spreading or reflexed. The series are of about equal length, thus differing from the *Ratibida-Dracopis* type. In *Echinacea* the inner series is attenuated and often shows a transition into the pales, as exemplified in *E. paradoxa.*

The involucres of *Balsamorhiza* and *Iostephane* differ from those of the other genera studied in that the outer series of bracts is usually much larger than the inner series. The bracts often become foliaceous and extend beyond the disk, a condition which reaches its greatest degree of development in *Bal-*

samorhiza Bolanderi, B. deltoidea, and *B. macrolepis.* Chrysopetala, a subgenus of *Iostephane,* is an exception, its involucre being of the helianthoid type. There is so much variation in the size of the bracts in this type that the character is of value only in specific diagnosis.

In *Zaluzania* the bracts are two or three seriate, and are graduated but never exceed the disk in length. The outer series is herbaceous, while the inner series often becomes subherbaceous or subcoriaceous, but not membranaceous. The involucre in this genus is of little value for specific characters.

The involucre in the genus *Greenmaniella* is similar to that of *Zaluzania* but in the former the bracts of the inner series are distinctly membranaceous and marked by six or more conspicuous brownish-resinous parallel nerves. This character is also present but less pronounced in the outer series. The membraneous nature of the inner involucral bracts, as well as the pales, presents a character by which these two genera may be readily distinguished.

The Receptacle and Pales.—The pales (bracts of the receptacle) are quite similar in all the genera studied and of little importance in generic differentiation; hence they may be discussed as a part of the receptacle rather than treated separately. The form of the receptacle falls into three categories, namely, (1) the columnar; (2) the conical; and (3) the broadly convex.

The columnar type of receptacle is typified in *Ratibida, Dracopis,* and also in the Laciniatae, Heliopsidae, and Laevigatae sections of the genus *Rudbeckia.* It reaches its highest degree of development in *Rudbeckia maxima,* where it often attains a length of 5 cm.; the maximum length in *Ratibida* is 3 to 3.5 cm., as in *R. columnaris* and *R. peduncularis.* In *Ratibida* and *Dracopis* the receptacle is narrowly cylindrical from the base upwards, whereas in *Rudbeckia* it becomes broadened somewhat towards the base. In *Ratibida* and *Rudbeckia* the pales are deciduous from the receptacle after maturity, this being more pronounced in *Ratibida,* and they are bordered along each margin by a large elongated brownish or purplish

resin duct. In the columnar sections of *Rudbeckia* the pales are absent, or if present represented by fine brownish lines.

Echinacea, Iostephane, Zaluzania, Greenmaniella, and a majority of the species of *Rudbeckia* fall into the second category with conical receptacles. The maximum development is attained in *Echinacea* and the subgenus Euiostephane of *Iostephane.* The receptacle in *Echinacea* is elongated, 1–1.5 cm. high. In Euiostephane the receptacle is also conical, but the head appears hemispherical, due to the outer pales being longer than the inner. The pales of the two latter genera are stout and terminate in straight or slightly curved spiny tips. This is more pronounced in *Echinacea,* where the stout slender spiny tips extend beyond the corollas, thus giving the head an echinate appearance. The pales of *Zaluzania* are without characters of any generic significance, but the pales of *Greenmaniella* are thin and membranaceous and marked by several brownish parallel veins, a type of pale rather unusual for the Verbesininae.

Balsamorhiza is characterized by a broadly convex receptacle, a type also characteristic of *Wyethia,* a pappose genus of the Verbesininae. In both of these genera the heads are very large and so very similar that for one not familiar with the two genera it is necessary to examine the achenes before one is certain as to the genus. The large broadly convex receptacle of *Balsamorhiza* may distinguish it from other epappose genera of the Verbesininae.

Corollas.—The ray-flowers are of two types, styliferous, as in *Balsamorhiza, Greenmaniella,* and *Zaluzania,* or without styles, as in *Echinacea, Dracopis, Iostephane, Ratibida,* etc. This difference, since it is a constant character and since it results in either fertile or sterile achenes of the ray-flowers, serves as a major factor in separating these genera into two main divisions. The lamina and tube present no marks of generic importance. The rays are present in all the species of these genera except *Zaluzania discoidea, Z. Pringlei,* and *Balsamorhiza invenusta,* and here the characters of the achene and disk-corolla are sufficient to identify the genus. In these

genera the ligules are commonly yellow. In *Echinacea* and *Iostephane* the rays in the majority of the species are purple, but in *Ratibida* they are often dark purple blotched at the base.

The form and size of the disk-corollas are very uniform for each genus and present good generic characters in a majority of cases (pl. 5), but they are of minor importance for species characters. Two main groups may be recognized: (1) disk-corollas with a narrowly constricted tube which expands above into a broad tubular or tubular-campanulate throat and the 5-lobed limb; and (2) disk-corollas without a definite tube.

Balsamorhiza, Greenmaniella, Dracopis, Iostephane, and *Zaluzania* fall within the first group. *Zaluzania* differs from these genera in that the base of the tube is expanded so as to completely cap the crown of the achene. This and the epappose achenes and the styliferous ray-flowers are the outstanding characters of the genus. This type of disk-corolla is also found in a few species of *Viguiera.* A major difference between *Greenmaniella* and *Zaluzania* is also found in the base of the corolla-tube. In the former the base of the tube is narrow and seated inside the cup-like crown of the achene. The lower portion of the throat of the corolla in *Balsamorhiza* and *Dracopis* is often enlarged somewhat on one side, but this varies so as to be of little generic or specific importance.

Echinacea and *Ratibida* belong to the second group. The disk-corolla in *Echinacea* is enlarged at the base into a bulb-like structure which contracts above into the cylindrical, 5-lobed corolla-tube. The stamens are attached near the swollen base of the corolla. *Ratibida* differs from *Echinacea* in that the corolla is narrowed slightly at the base and then expands above into the inflated corolla-tube. The stamens, as in *Echinacea,* are also attached near the base of the corolla.

The anthers and style appendages conform to those of the Verbesininae.

Achenes.—The achenes are relatively uniform in each genus included in this study. The ray-achenes are trigonal, but in *Echinacea, Ratibida,* and *Rudbeckia* they are never fully enough developed to be of any taxonomic importance. In

Zaluzania mollissima, Z. subcordata, and *Z. augusta* the pappus of the ray-achenes furnishes useful supplementary characters in the key to the species.

The disk-achenes are more or less characteristic for each genus (pl. 5). Comparative studies are based on (1) the outline in transverse section, and (2) the nature of the crown of the achene. The general types of outline are terete, rhomboidal, and quadrangular. The majority of the genera fall in the two latter categories. The pappus, when present, is very rudimentary in comparison with that found in other Heliantheae. It varies from a toothed crown in *Echinacea,* two awn-like teeth in *Ratibida,* to the shallow cup- or disk-like crowns in *Dracopis* and *Greenmaniella.*

Dracopis is characterized by a small, black, terete, linear-cuneate achene which is minutely striated and conspicuously transversely wrinkled. The apex of the achene is bordered by a minute, brownish, disk-like crown, this type being particularly characteristic of the genus. These characters, however, are based upon the mature achene. The transversely wrinkled surface is demonstrated to a lesser degree in many species of *Rudbeckia.* The ray-achenes in *Dracopis* are rhomboidal, pubescent, and also shorter and thicker than those of the disk; the crown also has a more pronounced cup-like pappus than the disk-achenes.

The achene of *Greenmaniella* also approaches the terete type of outline. In transverse section it is broadly subangulate to subterete at maturity. In longitudinal outline it is subfusiform, that is, the broadest part is in the upper half, from which it narrows gradually towards the apex and the base. The achene is terminated by a shallow cup-like pappus with knob-like projections at the angles. The achenial character is of generic importance, since it is quite unlike those of other genera with fertile ray-flowers.

In *Echinacea, Iostephane,* and *Zaluzania* the achenes have a general rhomboidal outline in transverse section. The achene of *Zaluzania* is capped by the expanded base of the corolla-tube, and as a result no pappus is ever present, a character which

readily distinguishes this genus from all others in this study. In *Iostephane* the achene is slightly rounded at the point of insertion of the corolla. A pappus is normally absent, but if present it is represented by one or two minute paleaceous setae. The achene in *Echinacea* terminates abruptly in the jagged and toothed border surrounding the concave depression at the summit where the bulbous base of the corolla is seated. The angle facing the subtending pale has developed an elongated tooth in a majority of the species.

The achenes of *Ratibida* differ from those of the other genera in being laterally flattened or compressed-rhomboidal. In the former type, which is the more common, the pappus is composed of two awn-like teeth on each edge of the achene. The flattened edges are also more or less winged, as in *R. peduncularis.* The latter type of achene is less compressed and without a pappus, as in *R. pinnata* and *R. mexicana.*

Balsamorhiza differs from the above genera in that the achenes are from 6 to 8 mm. long and quadrangular in cross-section. Their length is two to three times that of the average achene, which, with the quadrangular outline and the absence of a pappus, is sufficient to distinguish the achenes of this genus from any other epappose genus of the Verbesininae.

PROBABLE PHYLOGENY

A discussion of the evolutionary development of this group of genera, as of any large group of closely related genera, must be more or less hypothetical. Nevertheless, from the foregoing discussion a probable line of descent may be surmised.

The ancestral stock of *Balsamorhiza, Iostephane, Zaluzania, Ratibida, Dracopis,* and *Echinacea,* within the subtribe Verbesininae, probably has been evolved from two generic complexes, namely, the *Viguiera* complex and the *Echinacea-Rudbeckia* complex. The former complex may be defined as including those pappose genera, probably extinct, which were similar to extant genera, *Helianthus, Viguiera, Tithonia,* etc. *Balsomarhiza, Iostephane, Zaluzania,* and probably *Greenmaniella,* have been derived from this complex. The *Echinacea-*

Rudbeckia complex probably comprised plants with a more or less columnar or conical receptacle similar to the present species of *Rudbeckia, Echinacea,* etc. The ancestry of *Dracopis, Rudbeckia, Ratibida* and *Echinacea* may be sought within this complex.

Iostephane has taken its origin from a helianthoid ancestor. Its evolution has progressed along two lines, one terminating in the subgenus Chrysopetala, the other in Euiostephane. The former is more closely related to *Helianthus* in the nature of the involucre, receptacle, achenes, and the corolla. Euiostephane is less closely connected, its large conical receptacle, echinate pales, and purple rays showing a more remote relationship. It is also probably an older entity. The presence of minute setose squamellae, which is uncommon, indicates a relationship with this complex. The genus is confined to the Mexican Plateau, an old region geologically speaking.

The relationships of *Zaluzania* are with the *Viguiera* complex, but its exact ancestral stock is somewhat in question. Evidence at present points to affinities with a *Viguiera-Gymnolomia* type of ancestor. The fertile ray-flowers of *Zaluzania,* along with other evidence such as the woody or suffruticose habit, the simple entire leaves in a majority of the species, and a distribution chiefly confined to the Mexican Plateau, all point to a primitive rather than a more recent group. The herbaceous species of this genus, with lobed or pinnatisect leaves, are of more recent origin. The absence of a pappus in the disk-flowers is probably due to displacement by the dilated corolla base. This is further borne out by the presence of a pappus in the ray-flowers, in which the corolla base is not dilated.

The affinities of *Greenmaniella* are in doubt since its present position in the tribe is not certain. The membranaceous nature of the involucre and pales indicates affinities other than the Verbesininae, but the determination of its exact relationship must await the collection and study of additional material.

Balsamorhiza is closely related to *Wyethia* from which it has probably been derived. The more primitive species of this

genus, as in many species of *Wyethia,* have entire, more or less ovate, pinnate, basal leaves, with subscapose stems. These species are also more aggressive and more widely distributed. *Wyethia* has affinities with the *Viguiera* complex, but this genus is of more recent origin.

The *Echinacea-Rudbeckia* complex is confined chiefly to the United States. The following theory as to their origin, based on their geographical distribution, seems plausible. This group of genera probably evolved from a similar group of plants that originated on the Appalachian-Ozarkian Upland, a region exposed since the close of the Paleozoic. A discussion of each genus, which follows, furnishes the basis for this assumption.

Echinacea is perhaps the older of these genera. Five of its six species occur on the Appalachian-Ozarkian Upland. The two most primitive species, *E. laevigata* and *E. purpurea,* are confined to this region. *Echinacea laevigata* occurs along the uplands east of the Alleghenies from eastern Pennsylvania to Georgia. This species is uncommon within its range. *Echinacea purpurea* ranges from Georgia north and west to Kentucky, and enters the Ozarkian Upland by way of southern Illinois. These two latter species are 2 to 4 feet tall, and more or less branched with leafy stems.

Echinacea paradoxa is confined to the Ozarkian Upland and the Cretaceous uplands of eastern Oklahoma and Texas. *Echinacea pallida,* a more recent species, occurs on these uplands, and has also migrated into the surrounding prairies of more recent geological history. This species has given rise to *E. angustifolia* on the dry plains to the west, extending from the Dakotas south to western Texas. These three species are more recent, due to (1) their adaptation to a drier climate of the prairies and plains, (2) their occurrence in a more recent territory, and (3) more hispid pubescence with smaller leaves and rather low, somewhat subscapose stems. The pronounced spiny pales of *Echinacea,* the corolla with a bulbous base, unlike that of any other genus, are all probably primitive characters.

Rudbeckia and *Echinacea* have evolved from a similar ancestor, but the former is of more recent origin. The area

of present development of the later species of *Rudbeckia* extends along the coastal plain from Virginia to Texas. The center of distribution includes the Appalachian-Ozarkian Upland and the coastal region from Virginia to Texas. The epappose Hirtae and Bicolores sections of this genus are of more recent development. The species of the former section are aggressive and quite nascent.

The center of distribution of the columnar species of *Rudbeckia* extends from Alabama to the Ozarkian Upland, Texas, and westward, a few species reaching the Pacific coast. It is quite evident that *Rudbeckia* has evolved along two lines, one giving rise to the type with the columnar receptacle, the other to the type with the conical receptacles. The former has developed from the western extension of this upland, and the latter from the Appalachian region. *Dracopis* has been evolved from somewhere along the columnar receptacle branch.

The center of distribution of *Ratibida* is in the region of Nebraska, since its greatest development is from the Dakotas and Montana along the dry plains to Texas, New Mexico, and northern Mexico. This is perhaps the latest genus of the *Echinacea-Rudbeckia* complex. Since *Dracopis* and *Ratibida* have many characters in common, it is probable that they have had a common ancestor. Evidence in favor of the more recent origin of this genus is to be found in (1) the distribution in a more recent territory, geologically speaking, (2) the pinnate leaves, (3) the specialized seed dispersal, and (4) the aggressive and weedy nature of many of the species.

GENERAL DISTRIBUTION

The geographical distribution of the several genera comprised in this study, except in the case of *Zaluzania,* is coincident for the most part with certain botanical regions in the United States and in Mexico. *Balsamorhiza, Echinacea,* and *Ratibida* are native of the United States. The first-mentioned genus is confined to the northwestern states, whereas the other two genera are confined chiefly to the central and west-central states. The geographical range of *Ratibida* extends southwestward into northern Mexico. *Iostephane, Greenmaniella,* and

Zaluzania are mainly of Mexican distribution. Two species of *Zaluzania,* however, are extralimital; *Z. Grayana,* for example, reaches its northern limits in Arizona, while *Z. Sodiroi* is known only from Ecuador, South America. A more detailed distribution of each genus is given in the taxonomic treatment of the respective groups.

Abbreviations

The following abbreviations are used for the various herbaria cited in the taxonomic portion of this study:

F = Herbarium of the Field Museum of Natural History.
G = Gray Herbarium of Harvard University.
K = Herbarium of the Royal Botanic Gardens, Kew.
M = Herbarium of the Missouri Botanical Garden.
NY = Herbarium of the New York Botanical Garden.
Ph = Herbarium of the Academy of Natural Sciences, Philadelphia.
RM = Rocky Mountain Herbarium, University of Wyoming.
U CAL = Herbarium of the University of California.
US = United States National Herbarium.
WU = Herbarium of Willamette University.

Part II. Taxonomy

KEY TO THE GENERA

A. Ray-flowers without styles.
B. Receptacle columnar, cylindric, or conic-cylindric at maturity.
C. Receptacle columnar; bracts of the involucre biseriate, the inner series one-half or less as long as the outer.
D. Mature achenes terete, transversely wrinkled; leaves simple..... *Dracopis*
DD. Mature achenes compressed-rhomboidal or laterally flattened, smooth; leaves pinnate.. *Ratibida*
CC. Receptacle cylindric or conic-cylindric; bracts of the involucre bi- to tri-seriate, of about equal length.......................... *Rudbeckia*
BB. Receptacle conical.
E. Achenes with the crowns slightly rounded, epappose or with a few minute caducous squamellae......................... *Iostephane*
EE. Achenes terminating abruptly into a truncate, toothed crown.
F. Corolla expanded below into a bulb-like base, contracted above into the cylindrical corolla-tube; pales with stout subuliferous apices .... *Echinacea*
FF. Corolla tubular; pales acute......................... *Rudbeckia*

AA. Ray-flowers styliferous.

G. Pales firm, subherbaceous to subcoriaceous; mature disk-achenes linear-oblong, rhomboidal or quadrangular; epappose.

H. Base of the disk-corolla dilated and capping the achene; receptacle conical; heads small to medium (disk 0.5–1 cm. broad), usually in corymbose or corymbose-paniculate clusters .... *Zalusania*

HH. Base of disk-corolla narrow; receptacle broadly convex; heads large (disk 2–4 cm. broad), usually solitary...... .... *Balsamorhiza*

GG. Pales membranaceous with several brownish-resinous parallel nerves; mature disk-achenes subfusiform, subterete; pappus a shallow cup-like crown with knob-like projections at the angles.. *Greenmaniella*

RATIBIDA Raf.

History.—The name *Ratibida* was proposed by Rafinesque[1] and a brief description of it was published in his 'Flora Ludoviciana' in 1817. The genus was based on *Rudbeckia columnaris* Pursh[2] of 1814. Pursh's characterization is identical with that of *Rudbeckia columnaris* Sims[3] in 'Curtis' Botanical Magazine' which appeared in 1813. Sims' description is accompanied by an excellent illustration, hence there can be no doubt as to the identity of the plant concerned. Furthermore, Rafinesque in his 'Flora Ludoviciana' states that "all the species with naked seeds as *R. pinnata &* must form my genus *Obelisteca,* and those with a simple perianthe, such as *R. columnaris* Pursh, my genus *Ratibida.* Raf." Moreover, in 1818, he[4] writes briefly of this genus; and in the following year he[5] published a full description of it in the 'Journal de Physique' where *Rudbeckia columnaris* Pursh is given as the name-carrying synonym.

The name *Rudbeckia columnifera* Nutt.[6] was first published in 'Fraser's Catalogue' in 1813. The description accompanying it is so indefinite that the name *R. columnifera* may be re-

[1] Rafinesque, C. S., Florula Ludoviciana. p. 73. 1817.

[2] Pursh, F., Fl. Am. Sept. 2: 575. 1814.

[3] Sims, J., in Curt. Bot. Mag. 39: *pl. 1601.* 1813.

[4] Rafinesque, C. S., in Am. Month. Mag. 268. 1818.

[5] Rafinesque, C. S., in Jour. Phys. & Chem. 89: 100. 1819.

[6] Nuttall, T., in Fraser's Cat. no. 75. 1813 [Reprint in Pittonia 2: 118. 1890].

garded as a *nomen subnudum.* Nuttall[7] himself in the 'Genera of North American Plants' in 1818 abandoned his name *R. columnifera* and recognized *Rudbeckia columnaris* Pursh.

The first description of *Lepachys* Raf. immediately follows that of *Ratibida* Raf. in the 'Journal de Physique' in 1819. It was based upon *Rudbeckia pinnata* Vent. It has since been regarded as congeneric with *Ratibida* Raf. Therefore, according to the International Rules of Botanical Nomenclature, *Ratibida* becomes the valid generic name with *Ratibida columnaris* as the type species.

In 1825 Cassini,[8] in 'Dictionnaire des Sciences Naturelles,' described the genus *Obeliscaria* which is based on *Rudbeckia pinnata* Vent. DeCandolle[9] in the 'Prodromus' in 1836 recognized Cassini's genus and treated *Ratibida* and *Lepachys* as sections under *Obeliscaria.*

Don,[10] in Sweet's 'British Flower Garden,' in 1838, was the first worker to recognize *Ratibida.* Barnhart,[11] in 1897, was next to recognize the validity of this name, and *Lepachys* was rejected for reasons similar to those given above.

The genus *Lepachys,* with its three species and one variety, was treated by Torrey and Gray[12] in their 'Flora of North America' in 1842. *Rudbeckia Tagetes* James was transferred to *Lepachys Tagetes* by Gray[13] in 'Pacific Railroad Report' in 1856. The last species to be described was *Lepachys mexicana* Watson[14] in 'Proceedings of the American Academy' in 1888.

GENERAL MORPHOLOGY

Roots.—The root system of *Ratibida* is of two types, namely, a vertical tap-root, and a fibrous or fleshy fibrous spreading root system. The first type is represented in its best development by *R. Tagetes,* where the roots are long, slender, vertical,

[7] Nuttall, T., Gen. N. Am. Pl. **2**: 178. 1818.
[8] Cassini, M. H., in Dict. Sci. Nat. **35**: 272. 1825.
[9] DeCandolle, A., Prodr. **5**: 558. 1836.
[10] Don, D., in Sweet's Brit. Fl. Gard. II, **4**: 361, *pl. 361.* 1838.
[11] Barnhart, J. H., in Bull. Torr. Bot. Club **24**: 410. 1897.
[12] Torrey, J. & Gray, A., Fl. N. Am. **2**: 313. 1842.
[13] Gray, A., in Pacif. Rail. Rept. **4**: 103. 1856.
[14] Watson, S., in Proc. Am. Acad. **23**: 277. 1888.

and rather deep-seated. A less-developed form of the first type is found in *R. columnaris* and *R. peduncularis,* which have a narrow, conical tap-root soon tapering to a slender tip. In these species, the roots are shallow, the main body being usually less than 1 dm. in depth. Plants with this type of root are biennials or short-lived perennials. The more extensively developed root system of *R. Tagetes* is of perennial duration.

Ratibida pinnata and *R. mexicana* possess the shallow horizontally developed or rhizome-like root from which many stout fibrous secondary roots develop. These species are perennials.

Stems.—The stems are herbaceous, erect, simple, or branched, often copiously so, giving the plant a compact bushy appearance, as in *R. Tagetes.* The leafy branches terminate in naked peduncles of varying lengths. The strongly sulcate character of the stem and branches, with regular light green ridges and dark green grooves, is a marked feature of nearly all species of this group.

Leaves.—The leaves are alternate, the lowermost long-petiolate and the uppermost short-petiolate to sessile. The blades are pinnate-cleft, pinnate to bipinnatifid. The basal leaves in *R. mexicana* are lanceolate, those of the stem 3–5-pinnate-cleft. The leaves of *R. pinnata* and *R. mexicana* are distinctly triple-nerved. This character is less pronounced in the other species.

Pubescence.—The hirsute to strigose-hirsute type of pubescence is prevalent throughout the genus. The basal leaf-petioles and the lower parts of the stems are spreading-hirsute, exemplified by *R. mexicana, R. peduncularis,* and *R. pinnata.* The upper parts of the leafy stems, as well as the long naked peduncles, are strigose-hirsute, or less frequently strigose-hirtellous. The leaves are sometimes tuberculate-strigose-hirsute, as illustrated by *R. Tagetes* and *R. pinnata.* The pubescence of the leaves and stems is always interspersed with resinous glands or globules. On the stems this is more pronounced in the grooves, while the ridges are strigose-hirsute.

Inflorescence.—The heads are solitary on long naked peduncles terminating the leafy branches.

a. Involucre.—The involucral bracts are herbaceous and biseriate; those of the inner series are oblanceolate, scarcely longer than the pales or often somewhat shorter; those of the outer series are linear, reflexed or spreading, and from two to three times longer than the inner series. The involucre, while characteristic for the genus, presents few characters of value in specific differentiation.

b. Receptacle and Pales.—The narrow columnar type of receptacle is characteristic of all the species of *Ratibida.* This varies in length somewhat within the genus, but reaches its maximum development in *R. columnaris.*

The pales are densely crowded, more or less conduplicate. The apices are broadly apiculate-obtuse, with the tip incurved and densely velutinous, thus giving the heads a velvety aspect. A narrow fusiform resin duct along the edge of each pale is present in all the species except *R. mexicana.* The pales closely clasp the achenes so that upon drying after maturity they separate from the receptacle and fall with the ripened achene.

c. Corollas.—All the species of *Ratibida* have heterogamous heads with neutral ligulate florets and fertile disk-florets. The 5-lobed disk-corollas are inflated-tubular. The corollas of the ray-flowers are usually yellow, but the color varies in some species from yellow to bluish-purple. This is especially demonstrated in *R. columnaris,* in which the rays range from yellow, blotched with bluish-purple at the base or to the middle, to entirely bluish-purple. A similar color variation is also common in *R. peduncularis* and its variety. The rays are broadly oblong-elliptical, rotund-ovate to oblong-lanceolate, 2–3-denticulate, strongly spreading or reflexed, often cleft to the top of the achene.

d. Achenes.—The achenes of the disk-flowers in *Ratibida* are laterally compressed, with margins acute, or prolonged into a flattened edge, with margins distinctly pectinate-fimbriate, as in *R. peduncularis,* or fimbriate-ciliate, as in *R. columnaris* and *R. Tagetes;* the body of the achene is glabrous.

Pappus.—Pappus none, or consisting of two reduced awns, or of a small crown bordered by minute teeth.

Geographical Distribution.—The genus *Ratibida* is confined chiefly to the central United States, its center of distribution lying in the region of Nebraska and Kansas. The majority of the species are inhabitants of dry soils, but the species are generally quite adaptable and respond readily to a more favorable environment.

The species *R. columnaris,* native of the region from the Dakotas and Montana south to Texas and Mexico, has migrated since the development of the railroads into territory east, west, and southwest of its former range. The more favorable environment, especially in Missouri and Illinois, produces more vigorous plants than those growing in Texas, Oklahoma, etc.

Ratibida pinnata is confined chiefly to the prairie states. The remaining species are of a southwestern distribution; *R. Tagetes,* an inhabitant of dry plains, prairies, and rocky hillsides, ranges from Kansas and Colorado south to Texas and northern Mexico. *Ratibida peduncularis* and its variety *picta* inhabit the Gulf coastal region of Louisiana and Texas. *Ratibida mexicana,* the only Mexican species, inhabits cool slopes of the Sierra Madre Mountains of Chihuahua and Durango.

TAXONOMY

Ratibida Raf. Fl. Ludovic. p. 73. 1817; in Jour. Phys. **89**: 100. 1819; D. Don in Sweet's Brit. Fl. Gard. **4**: 361, *pl. 361.* 1838; Barnh. in Bull. Torr. Bot. Club **24**: 410. 1897; Britt. & Brown, Ill. Fl. ed. 1, **3**: 419. 1898, and ed. 2, **3**: 474. 1913; Small, Fl. Southeast. U. S. ed. 1, 1260. 1903, and ed. 2, 1260. 1913; Coult. & Nels. Bot. Rocky Mts. 545. 1909; Woot. & Standl. in Contr. U. S. Nat. Herb. [Fl. N. Mex.] **19**: 705. 1915; Rydb. Fl. Rocky Mts. 927. 1917; Small, Man. Southeast. Fl. 1428. 1933.

Lepachys Raf. in Jour. Phys. **89**: 100. 1819; Cass. in Dict. Sci. Nat. **26**: 3. 1823; Less. Syn. Gen. Comp. 225. 1832; Torr. & Gray, Fl. N. Am. **2**: 313. 1842; Gray, Manual, 225. 1848; Benth. & Hook. Gen. Pl. **2**: 366. 1873; Gray, Syn. Fl. N. Am. **1**^{2}: 263. 1884; Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. IV. Abt. 5, 233. 1890; Coult. in Contr. U. S. Nat. Herb. [Bot. West.

Texas] **2**: 215. 1892; Rob. & Fern. in Gray's Manual, ed. 7, 832. 1908; Rydb. Fl. Pr. & Pl. Cent. N. Am. 838. 1932.

Obeliscaria Cass. in Dict. Sci. Nat. **35**: 272. 1825; DC. Prodr. **5**: 558. 1836.

Herbaceous biennials or perennials arising from horizontal or vertical rootstalks. Stem simple or branched, erect or occasionally horizontally spreading, sulcate, marked by alternating light and dark green lines. Leaves alternate, pinnate, bipinnate, or lyrately pinnatifid, the basal sometimes lanceolate, serrate or entire, acute, strigose-hirsute, tuberculate-strigose-hirsute and interspersed with glandular punctae, especially on the lower surface. Heads radiate, solitary on naked peduncles, cylindrical, oblong-cylindrical to globose. Bracts of the involucre biseriate, herbaceous, linear to linear-lanceolate, the outer series twice or more the length of the inner. Receptacle columnar. Pales more or less conduplicate, obtusely apiculate to truncately apiculate, the tip incurved, a linear or elliptical brownish resin duct usually present along each margin, apex densely puberulent or velutinous, deciduous with the mature achenes. Disk-flowers with a very short tube, throat inflated-tubular, 5-lobed, glabrous; anthers sagittate at the base with ovate appendages; style-branches recurved or spreading, apex acute or rounded, densely puberulent to hirsutulous. Ray-flowers neutral, rays yellow or bluish-purple, 2–3-dentate, the corolla-tube short or obsolete. Achenes laterally flattened, compressed-rhomboidal in cross-section, sometimes ciliate or pectinate-fimbriate along the edges, otherwise glabrous; pappus when present coroniform or prolonged upwards on each edge, forming two awn-like teeth.

Type species: *R. columnaris* (Sims) D. Don in Sweet's Brit. Fl. Gard. **4**: 361, *pl. 361.* 1838.

KEY TO THE SPECIES

A. Achenes strongly compressed or flattened, inner wing fimbriate; pappus consisting of two tooth-like projections or a lacerate crown.

B. Heads globular or oblong; achenial crown yellowish, thickened, bordered by minute lacerate setae.................................*2. R. Tagetes*

BB. Heads cylindrical or columnar; pappus consisting of two persistent tooth-like projections.

C. Plants erect, leafy throughout............................1. *R. columnaris*
CC. Plants erect, horizontally spreading, or ascending, leafy below, terminating in a long naked peduncle.
D. Leaves bipinnatifid; achenes pectinate-fimbriate along both edges..3. *R. peduncularis*
DD. Leaves lyrately pinnate; achenes fimbriate-pectinate along the inner edge..................................3a. *R. peduncularis* var. *picta*
AA. Achenes compressed-rhomboidal, not winged; pappus absent.
E. Basal leaves pinnate; pales with a linear brownish resin duct along each margin; plants branched above....................4. *R. pinnata*
EE. Basal leaves lanceolate, entire; pales without resin ducts; plants unbranched..5. *R. mexicana*

1. **Ratibida columnaris** (Sims) D. Don in Sweet's Brit. Fl. Gard. **4**: 361, *pl. 361.* 1838; Britt. & Brown, Ill. Fl. ed. 1, **3**: 419. 1898, and ed. 2, **3**: 474, *fig. 4454.* 1913; Small, Fl. Southeast. U. S. ed. 1, 1260. 1903, and ed. 2, 1260. 1913; Coult. & Nels. Bot. Rocky Mts. 545. 1909; Small, Man. Southeast. Fl. 1428. 1933.

Rudbeckia columnaris Sims in Curt. Bot. Mag. **39**: *pl. 1601.* 1813; Pursh, Fl. Am. Sept. **2**: 575. 1814; Nutt. Gen. N. Am. Pl. **2**: 178. 1818; Maund, Bot. Gard. **4**: *pl. 84;* n. 336. 1831; Hook. Fl. Bor.-Am. **1**: 311. [1834] 1840; Hemsl. Biol. Cent.-Am. Bot. **2**: 167. 1881.

Rudbeckia columnifera Nutt. in Fraser's Cat. n. 75. 1813.

Ratibida sulcata Raf. in Jour. Phys. **89**: 100. 1819.

Obeliscaria columnaris DC. Prodr. **5**: 559. 1836.

Lepachys columnaris (Sims) Torr. & Gray, Fl. N. Am. **2**: 315. 1842; Gray, Syn. Fl. N. Am. **1**^{2}: 264. 1884; Coult. in Contr. U. S. Nat. Herb. [Bot. West. Texas] **2**: 215. 1892; Rob. & Fern. in Gray's Manual, ed. 7, 833. 1908.

Ratibida columnifera (Nutt.) Woot. & Standl. in Contr. U. S. Nat. Herb. [Fl. N. Mex.] **19**: 706. 1915; Rydb. Fl. Rocky Mts. 927. 1917.

Lepachys columnifera (Nutt.) Macbr. in Contr. Gray Herb. No. 65: 45. 1922; Rydb. Fl. Pr. & Pl. Cent. N. Am. 838. 1932.

Stems one or more, erect, 2.5–12 dm. tall, branched, closely strigose-hirsute throughout with occasional interspersed resinous glands, sometimes hirtellous-strigose, lateral branches spreading; leaves including the petiole 3–15 cm. long, closely strigose-hirsute on both surfaces, interspersed by numerous punctate glands, pinnately cleft to the midrib into 5–13 linear,

narrowly lanceolate, oblong or oblong-lanceolate divisions, these entire or sometimes trifid, acute, 0.5–3 cm. long, 1–10 mm. broad; heads cylindrical, 1–5.5 cm. long, 7–10 mm. broad; outer bracts of the involucre linear, 4–12 mm. long, acuminate, the inner about 3 mm. long, strigose-hirsute; ray-flowers 3–7, rays yellow throughout, broadly oblong-elliptical, 1–2 cm. long, 0.6–1 cm. broad, trifid, tube and outer surface of ray puberulent; mature achenes compressed, 2 mm. long, glabrous, except the wing on the inner side, which is ciliate-fimbriate, pappus consisting of two tooth-like projections on each edge of the crown.

Distribution: Illinois to Minnesota and Montana, south to Texas and Mexico.

The following, selected from numerous specimens, are representative:

ILLINOIS: railroad, Edwardsville, Madison Co., June 26, 1891, *Eggert* (M).

MISSOURI: dry sandy ground, Hannibal, Marion Co., Aug. 7, 1912, *Davis 5114* (M); railroad tracks, Winfield, Lincoln Co., June 7, 1916, *Davis 1390* (M); common, introduced, Sheffield, Jackson Co., June 26, 1894, *Bush 157* (M); waste ground, Courtney, Jackson Co., July 7, 1894, *Bush 163* (M).

ARKANSAS: rocky open ground, Brentwood, Washington Co., July 7, 1915, *Palmer 8216* (M).

MINNESOTA: Brown Valley, Traverse Co., Sept., 1893, *Sheldon* (M); Glyndon, Clay Co., Sept., 1892, *Dewart* (M).

NORTH DAKOTA: Ryder, Ward Co., July 31, 1928, *Larsen 187* (M).

SOUTH DAKOTA: Brookings, Brookings Co., Aug. 7, 1893, *Thornber* (M); Iriquois, Kingsbury Co., Aug. 11, 1897, *Thornber* (M); plains and ravines, "Bad Lands," Cedar Pass, near Interior, Stanley Co., June 29, 1929, *Palmer 37528* (M); hillsides, Deadwood, Lawrence Co., July 13, 1913, *Carr 93* (M).

NEBRASKA: railroad tracks, Havelock, Lancaster Co., July 13, 1915, *Davis 7320* (M); field, 20 mi. west of Hastings, Adams Co., June 17, 1929, *Mathias 309* (M); Kearney, Buffalo Co., June 27, 1899, *Pammel* (M); Orella, Sioux Co., July 6, 1912, *Pool & Folsom* (M).

KANSAS: prairies near Spearville, Ford Co., Aug. 24, 1902, *Eggert* (M); Grinnell, Gove Co., July 15, 1872, *Redfield 485 (3503)* (M); common, near Ulysses, Grant Co., June 24, 1893, *Thompson* (M); Summit, 17 mi. east of Arriba, Marshall Co., June 30, 1926, *Heller 13975* (M); Paola, Miami Co., Aug. 20, 1884, *Oyster 4149* (M); east of Coffeyville, Montgomery Co., June 28, 1929, *Rydberg & Imler 366* (M); prairie, Rice Co., Aug. 23, 1895, *Hitchcock 267* (M); Manhattan, Riley Co., June, 1891, *Ellis* (M).

OKLAHOMA: sandy soil, 17 mi. n. Boise City, Cimarron Co., Aug. 22, 1927, *Stratton 444* (M); Norman, Nov. 10, 1914, *Emig 366* (M); Lawton, Comanche Co., Aug., 1903, *Duncan* (M); abundant in prairies, Sapulpa, Creek Co., July 22, 1894, *Bush 307* (M); 6½ mi. west of Buffalo, Harper Co., Aug. 20, 1927, *Stratton 399*

(M); Arbuckle Mts., near Davis, Murray Co., June 21, 1917, *Emig 772* (M); Muscogee, Muscogee Co., July, 1880, *Letterman* (M); prairies near Cora, Woods Co., May 28, 1913, *Stevens 764* (M).

TEXAS: Claude, Armstrong Co., June 25, 1902, *Reverchon 493* (M); common on prairies, San Antonio, Oct. 2, 1900, *Bush 1234* (M); Ridge Springs, 9 mi. south of Marathon, Brewster Co., July, 1921, *Ferris & Duncan 2838* (M); foothills below McKittrick Canyon, alt. 1650 m., Guadalupe Mts., Culberson Co., July 23, 1931, *Moore & Steyermark 3618* (M); prairies, Houston, Harris Co., May 24, 1915, *Palmer 7746* (M); prairies near Canadian, Hemphill Co., Aug. 10, 1900, *Eggert* (M); rocky open ground in canyon, Davis Mts., Jeff Davis Co., June 17, 1926, *Palmer 31021* (M); on prairies, Terrell, Kaufman Co., Oct. 22, 1902, *Reverchon 3337* (M); near Kerrville, Kerr Co., alt. 1600–2000 ft., June 12–19, 1894, *Heller 1850* (M); Lubbock, Lubbock Co., May 19, 1931, *Demaree 7706* (M); along railway near Amarillo, Potter Co., July 13, 1917, *Palmer 12535* (M); dry open plains, Canyon, Randall Co., June 3, 1918, *Palmer 13878* (M); sandy woods, Troupe, Smith Co., May 9, 1902, *Reverchon 3338* (M); Abilene, Taylor Co., May 22, 1902, *Tracy 7891* (M); Del Rio, Valverde Co., April 17, 1930, *Jones 25903* (M).

MONTANA: dry ground, Bozeman, Gallatin Co., July 26, 1905, *Blankinship 283* (M); Missoula, alt. 3000 ft., Aug. 2, 1909, *M. E. Jones* (M).

WYOMING: Mammoth Hot Springs, Aug. 22, 1892, *Mulford* (M); waste ground, Laramie, Albany Co., alt. 7300 ft., July 27, 1929, *Goodman 226* (M).

COLORADO: near Boulder, alt. 5700 ft., July 8, 1920, *Hanson C139* (M); prairie near Denver, Denver Co., alt. 5300 ft., July 14, 1917, *Clokey 2819* (M); Manitou, El Paso Co., Aug., 1884, *Letterman* (M); near Cañon City, Fremont Co., July 8, 1873, *Brandegee 757* (M); Fort Collins, Larimer Co., alt. 5000 ft., July 9, 1896, *Baker* (M); near Pueblo, Pueblo Co., June 29, 1929, *Mathias 526* (M); Ft. Lupton, June 29, 1913, *Johnston 217* (M); Wray, Yuma Co., July, 1919, *Eggleston* (M).

NEW MEXICO: White Mountains, Lincoln Co., alt. 6700 ft., July 31, 1897, *Wooton 261* (M); Nara Visa, Quay Co., Aug. 1, 1911, *Fisher* (M); near Pecos, San Miguel Co., Aug. 20, 1908, *Standley 5124* (M); north of Glorieta, Aug. 24, 1908, *Standley 5279* (M).

MEXICO: COAHUILA—Chojo Grande, 27 miles southeast of Saltillo, Aug. 29, 1904, *Palmer 345* (M); CHIHUAHUA—near Colonia Garcia in the Sierra Madres, alt. 7500 ft., Aug. 5, 1899, *Townsend & Barber 230* (M); SAN LUIS POTOSI—Nov., 1910, *Purpus 4768* (M); NUEVO LEON—near Monterey, alt. 550 m., July, 1911, *Arsène 2603* (M).

1a. forma **pulcherrima** (DC.) W. M. Sharp, comb. nov.

Obeliscaria pulcherrima DC. Prodr. **5**: 559. 1836.

Ratibida columnaris var. *pulcherrima* (DC.) D. Don in Sweet's Brit. Fl. Gard. II. **4**: 361, *pl. 361.* 1838; Coult. & Nels. Bot. Rocky Mts. 545. 1909.

Lepachys columnaris var. *pulcherrima* (DC.) Torr. & Gray, Fl. N. Am. **2**: 315. 1842; Gray, Syn. Fl. N. Am. **1**^{2}: 264. 1884; Rob. & Fern. in Gray's Manual, ed. 7, 833. 1908.

Ratibida columnifera var. *pulcherrima* (DC.) Woot. & Standl. in Contr. U. S. Nat. Herb. [Fl. N. Mex.] **19**: 706. 1915.

Habit, foliage, pubescence, etc. identical with the species; ray-flowers bluish-purple, or bluish-purple blotched at the base.

Distribution: same as the species.

The following, selected from numerous specimens, are representative:

MISSOURI: waste ground, Sheffield, Jackson Co., June 17, 1918, *Bush 8407* (M).

ARKANSAS: open ground, Fulton, Hempstead Co., June 17, 1915, *Palmer 8024* (M); railroad near Mandeville, Miller Co., June 10, 1898, *Eggert* (M).

NORTH DAKOTA: Ryder, Ward Co., July 31, 1928, *Larsen 194* (M).

SOUTH DAKOTA: Iriquois, Kingsbury Co., Aug. 1, 1892, *Thornber* (M).

NEBRASKA: sand hills, Cherry Co., 1892, *Smith & Pound 145* (M); Lincoln, Lancaster Co., July 11, 1899, *Hedgcock* (M); common in prairies, Sioux Co., July–Aug., 1927, *Kramer 60* (M).

KANSAS: Ellis Co., June 26, 1885, *Kellerman* (M); New Ulysses, Grant Co., June 24, 1896, *Thompson* (M).

OKLAHOMA: Frederick, Tillman Co., July 5, 1903, *Duncan 28* (M).

TEXAS: Bryan, Brazos Co., May 27, 1915, *Palmer 7792* (M); vicinity of Brownsville, Cameron, Co., Aug. 1–5, 1921, *Ferris & Duncan 3113* (M); railroad near Longview, Gregg Co., June 7, 1899, *Eggert* (M); near Lubbock, Lubbock Co., May, 1930, *Demaree 7706a* (M); Corpus Christi, Nueces Co., May, 1913, *Orcutt 5821* (M); sandy woods, Troupe, Smith Co., May 9, 1902, *Reverchon 3338* in part (M); Austin, Travis Co., Aug., 1882, *Kellerman* (M); Del Rio, April 20, 1930, *Jones 25904* (M).

WYOMING: Willow Creek, July 20, 1894, *Nelson 570* (M); Manville, Niobrara Co., July 18, 1901, *Nelson* (M).

COLORADO: Fort Collins, Larimer Co., alt. 5000 ft., July 27, 1892, *Crandall* (M); Cheyenne Cañon, Colorado Springs, El Paso Co., Aug. 24, 1915, *Drushel 4191* (M); Denver, Denver Co., Aug. 5, 1885, *Fritchey 167* (M); Pagosa Springs, Archuleta Co., Aug. 13, 1917, *Payson 1164* (M).

NEW MEXICO: valley of the Pecos, Aug. 13, 1847, *Fendler 387* (M); Nara Visa, Ouray Co., Sept. 19, 1910, *Fisher* (M); Mogollon Mts., on the middle fork of the Gila River, Socorro Co., Aug. 8, 1903, *Metcalfe 415* (M); Carson Forest, Rio Arriba Co., 2100 m., Aug. 14, 1924, *Eggleston 20562* (M); White Mts., Lincoln Co., alt. 6500 ft., July 30, 1897, *Wooton 247* (M); near Pecos, alt. 6700 ft., Lincoln Co., Aug. 15, 1908, *Standley 4925* (M).

MEXICO: NEUVO LEON—Carrizitos, May 28, 1847, *Gregg 810* (M); COAHUILA—Matamoros, April 12, 1906, *Tracy 8947a* (M).

2. **Ratibida Tagetes** (James) Barnh. in Bull. Torr. Bot. Club **24**: 410. 1897; Britt. & Brown, Ill. Fl. ed. 1, **3**: 419. 1898, and ed. 2, **3**: 475. 1913; Small, Fl. Southeast. U. S. ed. 1, 1260. 1903, and ed. 2, 1260. 1913; Woot. & Standl. in Contr. U. S. Nat.

Herb. [Fl. N. Mex.] **19**: 706. 1915; Rydb. Fl. Rocky Mts. 927. 1917.

Rudbeckia Tagetes James in Long's Exp. [Phila. ed.] **2**: 68. 1823.

Obeliscaria Tagetes (James) DC. Prodr. **5**: 559. 1836.

Lepachys columnaris var. *Tagetes* (James) Gray in Smithson. Inst. Contr. [Pl. Wright. pt. 1] **3**: 106. 1852.

Lepachys Tagetes (James) Gray in Pacif. R. R. Rept. **4**: 103. 1856; Gray, Syn. Fl. N. Am. **1**^{2}: 264. 1884; Coult. in Contr. U. S. Nat. Herb. [Bot. West. Texas] **2**: 215. 1892; Rydb. Fl. Pr. & Pl. Cent. N. Am. 838. 1932.

Stems slender, erect, the branches numerous, ascending, often giving the plant a bushy appearance, 1.5–4 dm. tall, strigose-hirsute, interspersed by numerous sessile glands especially in the grooves; leaves strigose-hirsute or tuberculate-strigose-hirsute on both surfaces, interspersed by numerous dark, resinous or punctate glands; basal and lower cauline leaves lanceolate, entire, or more often pinnately or bipinnately 3–5-cleft, 5–13 cm. long including the petiole, upper cauline usually 3–5-cleft into linear or linear-lanceolate segments, these 0.5–3 cm. long, 1–3 mm. broad, entire, acute; heads on peduncles 2–7 cm. long, numerous, often forming close clusters, globular to oblong, 0.8–1.5 cm. long, 8–10 mm. broad; ray-flowers 5–7, rays rotund-ovate to oblong-ovate, 4–6 mm. long, 3–5 mm. broad, trifid, reflexed, yellowish to bluish-purple, pubescent on the outer surface of the lamina; achenes ovate-oblong, 2–2.5 mm. long, winged on the inner edge, truncate, terminating in a thickened, usually yellowish crown which is bordered by minute lacerate setae, achenial body glabrous except along the fimbriate-ciliate wing.

Distribution: dry plains, prairies, and rocky hillsides, Kansas and Colorado, southward to Texas and northern Mexico.

KANSAS: Tribune, July 28, 1892, *Reed* (M); Johnson, Stanton Co., July 1, 1893, *Thompson* (M); prairie, Russell Co., July 13, 1895, *Hitchcock 268* (M); roadside, 7 mi. west of Meade, July 10, 1929, *Rydberg & Imler 807* (M); Wallace, Aug. 22, 1884, *Letterman* (M).

OKLAHOMA: on gypsum hill, near Hollis, Harmon Co., June 21, 1913, *Stevens 1080* (M).

TEXAS: dry ground, Amarillo, Potter Co., July 13, 1917, *Palmer 12534* (M); Tecline, Aug. 26–28, 1903, *Griffiths 5641* (M); Tascosa, June 24, 1902, *Reverchon 3340* (M); Sierra Blanca, July 3, 1895, *Mulford 260* (M); Amarillo, May 29, 1902, *Reverchon* (M); dry open ground along Rio Grande, near El Paso, El Paso Co., June 19, 1926, *Palmer 31100* (M); dry open plains, Channing, Hartley Co., June 18, 1918, *Palmer 14142* (M); near Lubbock, 1930, *Demaree 7528a* (M); Rio Grande Valley at Canutillo, El Paso Co., July 7, 1911, *Barlow* (M); near El Paso, 1849, *Wright 327* (M).

COLORADO: Iola, Gunnison Co., July 29, 1901, *Baker 667* (M); plains, July 4, 1901, *Eggert* (M); plains east of Denver, July 25, 1874, *Engelmann* (M).

NEW MEXICO: near Pecos, alt. 6700 ft., Aug. 15, 1908, *Standley 4950* (M); Mesilla Valley, Dona Ana Co., June 19, 1906, *Standley* (M); vicinity of Las Vegas, San Miguel Co., July 23, 1926, *Arsène & Benedict 15445* (M); Gray, Lincoln Co., alt. 6000–6500 ft., July, 1900, *Earle & Earle 150* (M); Santa Fe, alt. 7200 ft., July 8, 1897, *Heller 3829* (M); Santa Fe, July 14, 1880, *Rusby 78* (M); near Gray, Lincoln Co., alt. 6000 ft., July 12, 1898, *Skehan 32* (M); Las Cruces, Dona Ana Co., alt. 3900 ft., June 15, 1897, *Wooton 5* (M); San Miguel Co., 1897, *Brandegee 12051* (M); Sandia Mts., Allen's Ranch, alt. 7200 ft., Aug.–Sept., 1914, *Ellis 208* (M); waste fields, Santa Fe, July–Sept., 1847, *Fendler* (M); vicinity of Santa Fe, Galisteo, alt. 1865 m., Aug. 23, 1926, *Arsène & Benedict 15841* (M); Archer Ranch, Brazito, Dona Ana Co., May, 1926, *Child 573* (M); common in sandy soil, "Charius," July 20, 1846, *Wislizenus 25* (M); Mesilla Valley, Dona Ana Co., July 16, 1907, *Wooton & Standley 3315* (M).

MEXICO: State of Chihuahua, Valley of the Rio Grande, Paso del Norte, Sept. 14, 1886, *Pringle 1061* (M); Juarez, June 27, 1891, *Evans* (M).

2a. var. **cinerea** Standley in Muhlenbergia **5**: 30. 1909.

Habit similar to the species; stem and peduncles cinereous, densely matted tomentulose-hirsute; leaves grayish, densely hirsute-strigose, the segments of the upper leaves about 2 mm. broad.

Distribution: dry hillside near Pecos, San Miguel Co., New Mexico.

NEW MEXICO: near Pecos, alt. 6700 ft., Aug. 21, 1908, *Standley 5156* (M), ISOTYPE.

3. **Ratibida peduncularis** (T. & G.) Barnh. in Bull. Torr. Bot. Club **24**: 411. 1897; Small, Fl. Southeast. U. S. ed. 1, 1260. 1903, and ed. 2, 1260. 1913.

Lepachys peduncularis Torr. & Gray, Fl. N. Am. **2**: 315. 1842; Gray, Syn. Fl. N. Am. **1**[2]: 264. 1884; Coult. in Contr. U. S. Nat. Herb. [Bot. West. Texas] **2**: 216. 1892.

Stems erect or horizontally spreading, leafy below, terminat-

ing in a slender naked peduncle, 1–5 dm. long, spreading-hirsute below, strigose-hirsute to strigose-hirsutulous on the peduncles; leaves more or less bipinnatifid; the blade and petiole 2.5–15 cm. long, strigose-hirsute on both surfaces, interspersed with resinous glands below, segments 5–9, 0.5–5 cm. long, the bipinnate lobes 1–4 mm. broad, acute, the terminal segment sometimes broadly pinnately cleft; heads solitary, columnar, 1.5–4 cm. long, 8–11 mm. broad; the outer bracts of the involucre linear, 6–10 mm. long, acute, hirsutulous, the inner series about 2 mm. long; rays 0.5–2.5 cm. long, reflexed, yellow to bluish-purple, especially towards the base; achenes flat, 4 mm. long including the awn-like projections, the edges winged and conspicuously pectinate-fimbriate, otherwise glabrous.

Distribution: Gulf coastal region of Louisiana and Texas.

LOUISIANA: Cameron, July 4, 1903, *Tracy 8548* (G, M); Cameron Parish, July, 1903, *Cocks* (G).

TEXAS: near Corpus Christi, near sea-level, Nueces Co., May 28–31, 1894, *Heller 1789* (G, M); north of Corpus Christi, March 30, 1932, *Jones 29506* (M); Beeville, March 30, 1932, *Jones 29507* (M); "Felipe de Austin," 1835, *Drummond 108* (G); Hort. Cantab. anno 1848, *Wright* (G).

3a. var. **picta** (Gray) W. M. Sharp, comb. nov.

Lepachys peduncularis var. *picta* Gray in Smithson. Inst. Contr. [Pl. Wright. pt. 1] **3**: 107. 1852; Syn. Fl. N. Am. **1**^{2}: 264. 1884; Coult. in Contr. U. S. Nat. Herb. [Bot. West. Texas] **2**: 216. 1892.

Lepachys serratus Buckl. in Proc. Acad. Sci. Phila. **13**: 457. 1861.

Ratibida picta Small, Fl. Southeast. U. S. ed. 1, 1260. 1903, and ed. 2, 1260. 1913.

Leaves lyrately pinnate to pinnately parted, coarsely serrate to incised-serrate; achenes pronouncedly winged and pectinate-fimbriate along the inner edge, outer edge entire or coarsely ciliate; other characters as in the species.

Distribution: sandy woodlands of the Texas coastal region.

TEXAS: Tyler, Tyler Co., Sept. 20, *Reverchon 2229* (M); sandy woods, Hempstead, Waller Co., June 10, 1872, *Hall 336* (G, M); gulf coast, 1849, *Wright* (G); Hort. Cantab., 1848, *Wright* (G); oak woodlands, 30 mi. west of San Antonio, Sept. 18–19, 1879, *Palmer 718* (G); Victoria, April 18, 1905, *Tracy 8914* (G, M).

4. **Ratibida pinnata** (Vent.) Barnh. in Bull. Torr. Bot. Club **24**: 410. 1897; Britt. & Brown, Ill. Fl. ed. 1, **3**: 418. 1898, and ed. 2, **3**: 474. 1913; Small, Fl. Southeast. U. S. ed. 1, 1260. 1903, and ed. 2, 1260. 1913; Small, Man. Southeast. Fl. 1428. 1933.

Rudbeckia pinnata Vent. Desc. Pl. Nouv. Jard. Cels. 71, *pl. 71.* 1800; Sims in Curt. Bot. Mag. **49**: *pl. 2310.* 1822.

Lepachys pinnatifida Raf. in Jour. Phys. **89**: 100. 1819.

Obeliscaria pinnata (Vent.) Cass. in Dict. Sci. Nat. **35**: 272. 1825; **46**: 401. 1827; DC. Prodr. **5**: 558. 1836.

Lepachys pinnata (Vent.) Torr. & Gray, Fl. N. Am. **2**: 314. 1842; Gray, Manual, 225. 1848; Gray, Syn. Fl. N. Am. **1**^{2}: 263. 1884; Rob. & Fern. in Gray's Manual, ed. 7, 833. 1908; Rydb. Fl. Pr. & Pl. Cent. N. Am. 838. 1932.

Stems one or more from a horizontal rootstalk, stoutish, branched above, 4–12 dm. tall, spreading-hirsute below, strigose-hirsute to strigose-hirtellous above, intermixed with glandular globules; leaves strigose-hirsute to tuberculate-strigose-hirsute on both surfaces, interspersed with resinous glands; the basal long-petioled, pinnate, 1.5–3.7 dm. long, 3-7-pinnate, the upper short-petiolate, pinnate, 0.6–3 dm. long, leaf-segments 3–9, these linear-lanceolate to broadly lanceolate, triple-nerved, 2–9 cm. long, 0.4–2.5 cm. broad, sparsely serrate to entire, acute; heads oblong-cylindrical, 1.2–2.2 cm. long, 1–1.5 cm. broad; ray-flowers 5–10, rays oblong-lanceolate, 2–6 cm. long, 0.6–1.2 cm. broad, 2–3-dentate, puberulent on the outer surface; achenes 2–3 mm. long, glabrous; pappus absent.

Distribution: dry prairies and rocky glades, etc. Ontario to Georgia, west to Minnesota and Oklahoma.

The following, selected from numerous specimens, are representative:

ONTARIO: Windsor, July 27, 1901, *Macoun 34829* (M).

GEORGIA: high sandy bank of Flint River, Sumter Co., July 11, 1901, *Harper 1051* (M).

OHIO: prairie, Adams Co., Sept. 15, 1930, *Stephenson* (M).

KENTUCKY: Bowling Green, Warren Co., July 6, 1900, *Price* (M).

TENNESSEE: Columbia, Maury Co., 1891, *Shimek* (M); railroad near Dechard, Franklin Co., July 6, 1898, *Eggert* (M).

INDIANA: bank of the Wabash River, ¼ mi. east of Bluffton, Wells Co., July 31, 1906, *Deam 1370* (M).

WISCONSIN: near Lake Beulah, Walworth Co., Aug. 2, 1905, *Shannon 133a* (M).

ILLINOIS: near Tracy, Cook Co., Aug. 22, 1908, *Greenman 3624* (M); prairies near Oquawka, Henderson Co., *Patterson* (M); 7 mi. west of Kankakee, Kankakee Co., Aug. 3, 1912, *Sherff 1601* (M); prairie soil, Wabash, 6 mi. west of Decatur, Macon Co., July 12, 1915, *Clokey 2406* (M); dry rocky open ground, Golconda, Pope Co., Oct. 8, 1919, *Palmer 17003* (M); prairies, Winnebago Co., Aug., 1859, *Bebb 3508* (M).

MINNESOTA: Lake Shetek, Murray Co., July, 1922, *Metcalf 1896* (M).

IOWA: prairies, Armstrong, Emmet Co., Aug. 20, 1897, *Cratty* (M); Ames, Story Co., July 18, 1896, *Pammel & Ball 56* (M); common on prairies, near Dayton, Webster Co., Aug. 21, 1926, *Pammel 17* (M); dry prairie soil, Decatur Co., Aug. 17, 1904, *Anderson* (M); high prairie, Black Hawk Co., July 17, 1929, *Burk 556* (M).

MISSOURI: Shannon Co., July 22, 1891, *Bush* (M); near Independence, Jackson Co., July 9, 1894, *Bush 164* (M); dry open ground, Van Buren, Carter Co., July 6, 1914 *Palmer 6204* (M); in dry soil on rocky slope between Festus and Pevely, Jefferson Co., June 20, 1929, *Steyermark 1036* (M); near Allenton, St. Louis Co., July 20, 1893, *Letterman* (M); near Mark Twain Cave, Hannibal, Marion Co., July 25, 1918, *Davis* (M); near Eaglerock, June 27, 1897, *Bush 123* (M).

ARKANSAS: dry open ground, near Fulton, Hempstead Co., June 17, 1915, *Palmer 8037* (M); dry rocky hillside near Cotter, Baxter Co., June 16, 1914, *Palmer 6003* (M); Eureka Springs, Carroll Co., July 17, 1898, *Glatfelter* (M).

KANSAS: prairies, Shawnee Co., July 4, 1895, *Norton & Clothier 266* (M); Johnson Co., 1890, *Pellet* (M).

OKLAHOMA: in open shrubby woods, near Miami, Ottawa Co., Aug. 26, 1913, *Stevens 2283* (M).

5. **Ratibida mexicana** (Wats.) W. M. Sharp, comb. nov.

Lepachys mexicana Watson in Proc. Am. Acad. **23**: 277. 1888.

Stems one or more, unbranched, slender, 4–7 dm. tall, spreading-hirsute above; basal leaves lanceolate, 0.5–2.2 dm. long including the petiole, 1–3.5 cm. broad, serrate or serrate-crenulate, acute, attenuate at the base, hirsute on both surfaces, more densely so beneath, intermixed with globular, resinous glands; cauline leaves 3–5 pinnate-cleft or parted, 6–16 cm. long, the terminal lobe lanceolate, about one-half the length of the entire leaf, the lateral segments 1–3 cm. long, acute, sparsely serrate, surface as in the basal leaves; heads solitary on naked peduncles 1.5–5 dm. long, columnar, 1.8–2.5 cm. long, 1–1.3 cm. broad; pales without the brownish resin ducts; ray-flowers 8–15, rays yellow, oblong-lanceolate, 2–2.5 cm. long, 5–7 mm. broad, spreading, tube short, about 1 mm. long, pubescent on

the limb and outer surface; achenes about 3–4 mm. long, glabrous, pappus absent.

Distribution: cool slopes of the Sierra Madre Mts., Mexico.

MEXICO: CHIHUAHUA—cool slopes of the Sierra Madre, alt. 7000–9500 ft., Sept. 28, 1888, *Pringle 1648* (M); cool slopes of the Sierra Madre, Sept. 19, 1887, *Pringle 1305* (NY); Sierra Madre near Colonia Garcia, alt. 8000 ft., July 5, 1899, *Townsend & Barber 101* (M, NY); DURANGO—Sierra Madre, 30 miles north of Guanacevi, 8000–9000 ft., Aug., 18, 1898, *Nelson 4777* (NY).

IOSTEPHANE Benth.

History.—The genus *Iostephane* was first described by Bentham[1] in 'Genera Plantarum' in 1873. The species *Echinacea heterophylla* D. Don[2] was referred to and therefore must be interpreted as the type of the genus. Excellent illustrations of this species may be seen in the 'British Flower Garden' and also in Knowles & Westcott's 'Floral Cabinet,'[3] under *E. dubia.* Hemsley, in 'Biologia Centrali-Americana,'[4] recognized *Iostephane* and added a new species, namely, *I. trilobata* Hemsl.

Hoffmann[5] in Engler and Prantl's 'Die Natürlichen Pflanzenfamilien,' in 1890, briefly characterized the genus and related it to *Rudbeckia* and other allied genera which possess sterile ray-flowers and achenes without a pappus. At this time two species were recognized.

GENERAL MORPHOLOGY

Roots.—The root system consists of a fleshy spindle-shaped tap-root. The outer covering of the true tap-root is roughened by corrugated ridges of a bark-like structure, giving the root a woody appearance, but the interior tissue is fleshy. Its appearance, size, and structure suggest the tap-root of *Balsamorhiza.*

Stems.—The thickened tap-root gives rise to a slender, woody, stem-like body 1–4 inches long. The herbaceous stems arise from buds at the sides, just below the surface of the ground. Alternate scars along this narrowed underground

[1] Bentham, G., in Benth. & Hook. Gen. Pl. 2: 368. 1873.
[2] Don, D., in Sweet's Brit. Fl. Gard. II, 1: *pl. 32.* 1831.
[3] Knowles, G. B. & Westcott, F., Fl. Cab. 3: 163. 1839.
[4] Hemsley, W. B., Biol. Cent.-Am. Bot. 2: 168. 1881.
[5] Hoffmann, O., in Engler & Prantl, Nat. Pflanzenfam. IV. Abt. 5. 233. 1890.

structure seem to indicate that it is an erect, perennial, underground stem or rootstalk which has developed from the crown of the tap-root. The stems above ground are herbaceous, erect, semiscapose, and usually unbranched. The taller plants, as *I. heterophylla* var. *Dicksonii,* are branched.

Leaves.—The basal leaves are long-petiolate and very numerous; those of the stem are much reduced. Sometimes only a few bracts are present, and occasionally in *I. heterophylla* and *I. trilobata* the stem is destitute of leaves or bracts. The basal leaves in all species are either pandurate, lobed, or less often ovate, the pandurate outline being the most common type. The bases of the leaf blades are decurrent along the sides of the petioles. The venation is conspicuous in that one or sometimes two prominent veins branch off from the midvein in the broadened basal portion of the leaf, and above and below this point the venation is less prominent. The peculiar triple venation and the decurrent blades are characteristic for all species of the genus. The stem-leaves are usually bracteiform. The lowermost are sometimes leaf-like, and of a similar outline to the basal leaves, but they are always much reduced in size.

Pubescence.—The stem bears a strigose pubescence which is less abundant on the lower parts and gradually increases above. The peduncles are often densely pubescent just below the heads, especially so in *I. heterophylla* and *I. trilobata.* The stem in *I. heterophylla* var. *acutiloba* bears stout tuberculate-hispid hairs. The leaves are usually clothed by a tuberculate-hispid pubescence. Some specimens of *Iostephane trilobata* not only bear the above type of covering, but also hirsute trichomes.

Involucre.—The involucral bracts are usually in two, sometimes three, series. In the subgenus Euiostephane the outer bracts are longer than the innermost, often extending beyond the pales and the disk-flowers. In Chrysopetala the bracts are short, never extending beyond the disk-flowers. They are quite helianthoid, thus giving the head a very characteristic appearance. The bracts are foliaceous, lanceolate, or ovate-acuminate, the pubescence being similar to that of the foliage.

Receptacle.—Two types of receptacle occur within the genus, namely, (1) the Echinacea-Euiostephane type, and (2) the helianthoid type. The receptacle in Euiostephane is strongly conical and about 8 mm. high, in this respect being similar to *Echinacea.* The pales are stout, echinulate, and terminate in a sharp straight or incurved beak. The receptacle in Chrysopetala is little more than the expanded apex of the peduncle. The pales are weak, subcoriaceous, and sharply serrated towards the apex.

Ray-flowers.—The rays are neutral, with the achenes triangular in cross-section instead of rhomboidal as in the disk-flowers. The rays in Euiostephane are purple, oblong, and bidentate. Those of Chrysopetala, as the name signifies, are yellow and obovate. They are short, 7–12 mm. long, whereas those in the former subgenus are over 20 mm. long.

Disk-flowers.—The corolla of the disk-flowers is a typical helianthoid form, as contrasted with that of the *Rudbeckia* and *Echinacea* types. The tube is constricted into a narrow cylinder, extending about one-fourth the entire length of the corolla, then it expands abruptly into the upper cylindrical throat and 5-lobed limb, similar to that of *Helianthus.*

Geographical Distribution.—*Iostephane* is confined chiefly to central Mexico. The general range extends from southwestern Chihuahua southwards along the Mexican Plateau, especially at high elevations, to central and eastern Chiapas. The subgenus Chrysopetala occupies the extreme southeastern part of this range, with its northwestern limits in southeastern Puebla. Euiostephane extends from southern Chihuahua south to southern Puebla. *Iostephane heterophylla* is confined to south-central Mexico, ranging from southwestern San Luis Potosi south to Puebla, Morelos, and Michoacan. Its variety *Dicksonii* occurs from Chihuahua south to Puebla; whereas the variety *acutiloba* is known only from central Jalisco.

The species of this genus, so far as available records show, occur in altitudes above 5500 feet, the average elevation being from 6000 to 8000 feet above sea-level. One collection of *I. tri-*

lobata taken in the vicinity of Oaxaca was collected at an altitude of 9500 feet.

Iostephane is chiefly confined to the oak associations. The species occur on dry rocky hills in the open oak woodlands or among the denser stands of oaks. In this respect the habitat resembles that of certain species of *Echinacea*.

TAXONOMY

Iostephane Benth. in Benth. & Hook. Gen. Pl. **2**: 368. 1873; Hemsl. Biol. Cent.-Am. Bot. **2**: 168. 1881; Hoffm. in Engler & Prantl, Nat. Pflanzenfam. IV, Abt. 5. 233. 1890.

Herbaceous, semiscapose or leafy-stemmed perennials. Stems erect, from a thickened vertical rootstalk, simple or branched. Leaves alternate, radical or cauline, panduriform, trilobed-pandurate, ovate or broadly oblanceolate. Heads solitary, radiate, sometimes disposed in an open few-headed panicle. Involucre campanulate to hemispherical, bracts 2–3-seriate, herbaceous, lanceolate to ovate-oblong, acuminate, entire. Receptacle conical to slightly convex, paleaceous; pales coriaceous, entire to serrate towards the apex, broadly conduplicate, acute, apex straight or incurved. Ray-flowers sterile, disposed in a single row; rays purple or yellow. Disk-flowers perfect; corolla-tube constricted, expanded above into a broadened cylindrical throat and 5-lobed limb; stamens 5, anthers sagittate, the apical appendages ovate. Stigmatic branches acute or acuminate, reflexed or curled, pubescent on the outer surface. Achenes of the ray-flowers sterile; those of the disk fertile, rhomboidal to obcompressed, obtuse, glabrous or pubescent; pappus usually absent, or if present of a few minute paleaceous setae.

Type species: *Iostephane heterophylla* (Cav.) Benth. in Benth. & Hook. Gen. Pl. **2**: 368. 1873.

Subgenus I. **Euiostephane** W. M. Sharp, new subgenus.

Involucre hemispherical, 2–3 cm. in diameter, 15 mm. high; receptacle conical, 5–9 mm. high, 3–6 mm. broad at base; pales rigid, echinulate, entire, acute, stout at the apex; rays purple; disk-achenes oblong-obovate, rhomboidal, cinereous or brown-

ish strigose-pubescent; pappus usually absent, when present of minute paleaceous setae.

Subgenus II. **Chrysopetala** W. M. Sharp, new subgenus.

Involucre campanulate, 1–1.5 cm. in diameter, 6–10 mm. high; receptacle convex, 1–1.5 mm. high, 1–1.5 mm. broad; pales weak, cartilaginous, subechinulate, serrate; rays yellow; disk-achenes oblong-obovate, obcompressed, glabrous; pappus absent.

One species: *I. trilobata* Hemsl.

KEY TO THE SPECIES AND VARIETIES

A. Leaves broadly ovate to ovate-lanceolate, the upper little reduced........ .... *1a. I. heterophylla* var. *Dicksonii*

AA. Leaves ovate-pandurate to pandurate, trilobed or divided, the upper much reduced or lacking.

B. Rays purple; involucre hemispheric, 2–3 cm. in diameter; achenes pubescent.

C. Leaves pandurate, crenate, lateral lobes rounded; stems strigose-hirsute..*1. I. heterophylla*

CC. Leaves trilobed-pandurate, entire or dentate, the lateral lobes acute; stems tuberculate-hispid..............*1b. I. heterophylla* var. *acutiloba*

BB. Rays yellow; involucre campanulate, 1–1.5 cm. in diameter; achenes glabrous...*2. I. trilobata*

1. **Iostephane heterophylla** (Cav.) Benth. in Benth. & Hook. Gen. Pl. **2**: 368. 1873; Hemsl. Biol. Cent.-Am. Bot. **2**: 168. 1881.

Coreopsis heterophylla Cav. Icon. Pl. **3**: 34, *pl. 268*. 1795.

Rudbeckia napifolia HBK. Nov. Gen. & Sp. **4**: 244. 1820.

Echinacea heterophylla (Cav.) D. Don in Sweet, Brit. Fl. Gard. II. **1**: *pl. 32*. 1831.

Echinacea dubia Knowles & Westcott, Fl. Cab. **3**: 163. 1839.

Stems erect, scapose to subscapose, 5–9 dm. tall, unbranched or branched in the taller specimens, striate, strigose-hirsute, densely so near the heads; basal leaves panduriform, with a long constriction between the terminal and the lateral lobes, posterior lobes roundish, crenately toothed, more conspicuously so between the anterior and lateral lobes, 1–3.2 dm. long, 2–6 cm. broad, acute, strigose-tuberculate-hirsute especially on the upper surface, petioles 4–14 cm. long; cauline leaves few,

sessile, oblanceolate to lanceolate, 4–8 cm. long, entire, reduced to narrow lanceolate bracts above; heads solitary, radiate, including the rays 4–9 cm. broad; bracts of the involucre 1.5–2 cm. long, 5–6 mm. broad at the middle, oblong-lanceolate, attenuate, hirsute or hirsute-ciliate; pales 9–10 mm. long, coriaceous, acute at the apex, slightly serrate on the upper margins; rays 2.5–5 cm. long, 7–10 mm. broad, 12–15, bi-tri-dentate; disk-corollas sparsely pubescent on the expanded region; achenes oblong-obovate, about 4 mm. long, obcompressed, pappus absent, crown and body clothed by a brown strigose-hirsute pubescence, becoming less dense towards the base.

Distribution: on dry oak-covered hills, south-central Mexico.

MEXICO: SAN LUIS POTOSI—Alvarez, Sept. 5–10, 1902, *Palmer 65* (G, M, US); region of San Luis Potosi, Sept., 1876, *Schaffner 253* (G); MEXICO—"Santa Fe, Valley of Mexico," July 26, 1865–66, *Bourgeau 602* (G, US); "Santa Fe, Valley of Mexico," Aug. 22, 1903, *Rose & Painter 6493* (G, NY, US); among oak hills, near "El Oro," alt. 9000 ft., Oct. 8, 1902, *Pringle 9929* (G, M, US); dry woodland slopes, Sierra de las Cruces, Aug. 28, 1892, *Pringle 5249* (G, US); Sierra de las Cruces, Sept. 10, 1900, *Pringle 9276* (G); near San Angel, Aug., 1855, *Schaffner 58* (G); MICHOACAN—near Morelia, 1910, *Arsène 5518* (US); near Morelia, Sept. 5, 1909, *Arsène 2464* (US); PUEBLA—on "cerro Tepaxuchitl," alt. 6990 ft., vicinity of Puebla, Aug. 7, 1910, *Arsène & Nicolas 5408* (M, US).

1a. var. **Dicksonii** (Lindl.) W. M. Sharp, comb. nov.

Echinacea Dicksonii Lindl. in Edwards' Bot. Reg. N. S. 1: *pl. 27.* 1838.

Similar to the species, but usually more robust; stem 0.5–1 m. tall; basal and lower stem-leaves broadly ovate to ovate-lanceolate, 2–4.5 dm. long, 4–15 cm. broad, coarsely dentate, acute at the apex; heads including the rays occasionally 10 cm. in diameter.

Distribution: mountains of Mexico, from southern Chihuahua to Oaxaca.

MEXICO: CHIHUAHUA—southwest Chihuahua, Aug., 1885, *Palmer 333* (G, US); 15 mi. south of Guadalupe Calvo, alt. 7500–8000 ft., southwest Chihuahua, Aug. 22, 1898, *Palmer 4824* (G, US); DURANGO—region of Durango, Aug. 16, 1897, *Rose 2336* (G); JALISCO—in Sierra Madre, west of Bolonas, Sept. 15–17, 1897, *Rose 2969* (G, US); SAN LUIS POTOSI—region of San Luis Potosi, 22° N. lat., alt. 6000–8000 ft., 1878, *Parry & Palmer 470* (G); near Huajalote, *Ehrenberg 344* (G); HIDALGO—on Real del Monte, Hidalgo, *Coulter 374* (G); PUEBLA—vicinity of Puebla, Aug. 8, 1907, *Arsène 1056* (G, M, US); Mt. Orizaba, near Esperanza, Aug. 15, 1891, *Seaton 366* (G, US); vicinity of Esperanza, Sept., 1911, *Purpus 5694*

(G); MORELOS—Cuernavaca, Sept. 30, 1899, *Holway 3543* (G); OAXACA—"Serro San Felipe del agua," alt. 5700 ft., July 25, 1897, *Conzatti & Gonzales 404* (G).

1b. var. **acutiloba** W. M. Sharp, var. nov.[6]

Stems 4–9 dm. long, tuberculate-hispid, strigose; basal leaves trilobed-pandurate, the lateral lobes ½ as long as the terminal lobe, posterior lobes acute, entire, above tuberculate-hispid, beneath hispid; achenes oblong-obovate, 4–5 mm. long, canescent-strigose towards the summit; in all other characters similar to the species.

Distribution: known only from the state of Jalisco, under oaks on rocky hills.

MEXICO: JALISCO—near Guadalajara, Aug., 1893, *Pringle 4480* (G, M TYPE, US); "Rio Blanco," Aug., 1896, *Palmer 372* (G, NY, US).

2. Iostephane trilobata Hemsl. Biol. Cent.-Am. Bot. **2**: 169. 1881.

Rudbeckia chrysantha Klatt in Leopoldina **23**: 143. 1887.

Gymnolomia scaposa Brandegee in Univ. Cal. Publ. Bot. **4**: 93. 1910.

An herbaceous, strigose-pubescent perennial, 1.5–7 dm. tall; stems erect, one or more from a thickened rootstalk; basal leaves panduriform to ovate, 0.5–3 dm. long, 1.5–7 cm. broad, lateral lobes rounded, terminal lobe ovate to subovate, entire to sparsely serrate, hirsute-ciliate, strigose-hirsute below, strigose-tuberculate-hirsute to hirsute above; cauline leaves reduced, lowermost lanceolate, 6 cm. or less long, the uppermost reduced to sessile bracts subtending the branches; petioles of the basal leaves more than half the total length of the blade; heads solitary or disposed in an open few-headed panicle, including the rays 2–5 cm. broad, 6–13 mm. high; involucre campanulate; bracts of the involucre 2–3-seriate, lanceolate-acuminate, hirsute-pubescent; rays 6–13, yellow, 7–12 mm. long; achenes oblong-obovate, obcompressed, glabrous, epappose.

[6] **Iostephane heterophylla var. acutiloba** W. M. Sharp, var. nov., caulibus 4–9 dm. longis, tuberculato-hispidis, strigosis; foliis basalibus trilobato-panduratis, lobo terminali lobis lateralibus duplo longiore, lobis posterioribus acutis, integris, supra tuberculato-hispidis, subtus hispidis; achaeniis oblongo-obovatis, 4–5 mm. longis, ad apicem griseo-strigosis; cetera speciei similis.—Collected at Jalisco, Mexico, near Guadalajara, Aug., 1893, *Pringle 4480* (G, M TYPE, US).

Distribution: southern Mexico, in oak forests at elevations above 5000 feet.

MEXICO: PUEBLA—in oak forests, Coxcatlan, alt. 8000–9000 ft., Sept., 1909, *Purpus 4120* (G, M); OAXACA—in Sierra de Chavellinas, alt. 8500 ft., Oct. 19, 1894, *Pringle 4978* (G, M, US); 18 mi. southwest of the city of Oaxaca, alt. 5700–9500 ft., Sept. 10–20, 1894, *Nelson 1371a* (US); CHIAPAS—open forests, near Fenia, July, 1925, *Purpus 55* (G, US); near San Cristobal, alt. 7000–8800 feet, Sept. 18, 1895, *Nelson 3223* (G, US); without locality or date, *Ghiesbreght 101* (G); without locality, coll. of 1864–70, *Ghiesbreght 561* (G, M).

ECHINACEA Moench

History.—Previous to the time of Linnaeus, plants now considered to belong to the genus *Echinacea* were discussed by Plukenet[1] in 'Almagestum Botanicum' in 1696 and by Catesby[2] in 'Natural History' under the name *Chrysanthemum americanum.* Morison[3] in 'Plantarum Historia' in 1699 described *Dracunculus Virginianus latifolius.* Illustrations of both Catesby and Morison are identical with what are now considered to be *Echinacea.* Catesby's plate is apparently that which is now interpreted as *E. laevigata,* but his description accompanying the plate is somewhat vague. In 'Species Plantarum' Linnaeus[4] described an echinaceous plant under *Rudbeckia purpurea.* This name is based on *Chrysanthemum americanum* of Plukenet and of Catesby and on *Dracunculus Virginianus latifolius* of Morison. Necker[5] in 'Elementa' in 1790 described the genus *Brauneria.* No species are mentioned, but the generic description is practically the same as that of *Rudbeckia.* Moench[6] in 'Methodus Plantarum' in 1794 described the genus *Echinacea.* The name is derived from the Latin word "echinus," a hedge-hog, because of the prickly pales of the receptacle which give it a somewhat echinate appearance. His generic characters are clear-cut and comprehensive, the genus being based on *Rudbeckia purpurea* L. which, according

[1] Plukenet, L., Alm. Bot. 99. 1696; *ibid. pl. 21, fig. 1.* 1720.
[2] Catesby, M., Nat. Hist. Car. & Fla., ed. 3, 2: 59, *pl. 59.* 1771.
[3] Morison, R., Pl. Hist. pt. 3. sect. 6. 42, *pl. 9.* 1699.
[4] Linnaeus, C., Sp. Pl. 2: 907. 1753.
[5] Necker, J. D., Elem. Bot. 1: 17. 1790.
[6] Moench, C., Meth. Pl. 591. 1794.

to the International Rules of Botanical Nomenclature, becomes the type species of the genus *Echinacea*.

The botanists of the early and middle nineteenth century adopted the name *Echinacea*, while *Brauneria*, although four years older, remained in obscurity. Lessing,[7] Endlicher,[8] Meisner,[9] Lemaire,[10] and Bentham and Hooker[11] used the former name. Alphonse DeCandolle[12] recognized the name *Echinacea* in the 'Prodromus' and described under it four species. Torrey and Gray[13] in the 'Flora of North America' included three species in this genus. Thomas Nuttall[14] in 'Transactions of the American Philosophical Society' described three species, one of which, *E. pallida* Nutt., is valid at the present time, while the others have been reduced to synonymy or excluded from the genus. Gray,[15] in various editions of his 'Manual of Botany' from 1857–1889, recognized the genus *Echinacea*, listing two species. In the seventh edition, however, the name *Brauneria* is adopted, and four species are given. In the first edition of the 'Illustrated Flora of the Northern United States and Canada' Britton and Brown[16] used the name *Brauneria*, but in the second edition this is replaced by *Echinacea*. Small[17] in 'Flora of the Southeastern United States' recognized the genus *Brauneria* and included six species, four of which are retained in this monograph, one reduced to a variety, and the sixth being excluded.

GENERAL MORPHOLOGY

Stems.—The stems arise from rootstalks which die down each season and come up again in the spring, the parts above the ground thus being annual. The stems are of two types.

[7] Lessing, C. F., Syn. Gen. Comp. 225. 1832.
[8] Endlicher, S., Gen. Pl. 409. 1838.
[9] Meisner, C. F., Pl. Vasc. Gen. 202. 1839.
[10] Lemaire, C., Dict. Hist. Nat. 183–184. 1844.
[11] Bentham, G., & Hooker, J. D., Gen. Pl. **2**: 366. 1873.
[12] DeCandolle, A., Prodr. **5**: 554. 1836.
[13] Torrey, J., & Gray, A., Fl. N. Am. **2**: 305–306. 1842.
[14] Nuttall, T., in Trans. Am. Phil. Soc. II. **7**: 354. 1841.
[15] Gray, A., Man. of Bot., editions 1857–1889.
[16] Britton & Brown, Ill. Fl. ed. 1, **3**: 419. 1898, and ed. 2, **3**: 476. 1913.
[17] Small, J. K., Fl. Southeast. U. S. 1261–1262. 1903.

The first type is usually simple, sometimes once-branched, and one to three feet high, a single rootstalk sometimes giving rise to one or several stems. The second type is usually branched above one to many times, and bears a single head on each branch. The stems in *E. purpurea* commonly attain a height of four to five feet.

Leaves.—The leaves of *Echinacea* fall naturally into two groups, namely, the ovate and the lanceolate. The latter is the most common form in the genus. The basal leaves are usually long-petiolate, and the stem-leaves short-petiolate becoming sessile above. The leaves are normally three to five palmately veined. The primary veins run almost parallel in the narrow-leaved species.

Pubescence.—The pubescence within the genus is variable, each species having a characteristic form. For this reason it is one of the most outstanding taxonomic characters for the group and especially important for a satisfactory separation of the narrow-leaved species. In *Echinacea paradoxa* the pubescence is definitely strigose; in *E. pallida* it is hirsute; while in *E. angustifolia* it is tuberculate-hirsute to tuberculate-hispid. This last species is often referred to as having shaggy pubescence, the tuberculate-hispid hairs giving this appearance. *Echinacea laevigata* is the only glabrous species in the genus.

Involucral bracts.—The bracts of the involucre are usually in two to three series. In *E. paradoxa* the bracts show a marked transition into the pales, this transition indicating plainly the relation of pales to involucre. The pubescence on the bracts in all species is the same type as that of the leaves. When *E. purpurea* is grown in cultivation, abnormal heads are formed; the bracts of the involucre become leaf-like, and the receptacle somewhat elongated, thus showing a reversion perhaps to a more primitive form.

Receptacle and Pales.—The receptacle in *Echinacea* is distinctly conical. The pales on the receptacle are broad and persistent, terminating in coriaceous stiff or weak spines. The spiny apices extend from 1 to 4 mm. beyond the corolla, giving the head an echinate appearance.

Ray-flowers.—The ray-flowers are neutral and disposed in a single series. The rays are strap-shaped, one to three toothed, and in a majority of the species are sparsely pubescent on the outer surface. In *E. pallida* they are 4–9 cm. long and strongly reflexed. The predominating color is purple, but in *E. paradoxa* the rays are yellow.

The Disk-corolla.—The corolla is expanded below into a bulb-like base. This enlarged portion is sessile upon the top of the achene, this being one of the most important generic characters. The corolla contracts above into a cylindrical tube terminated by a five-lobed, erect or slightly ascending limb. The median vascular bundles of the corolla-lobes are absent, but there are five fused lateral bundles which divide at the sinuses and run along the margins of the corresponding lobes. The corolla is dark purplish as a rule. The stamens are five in number, united, and encompass the style. Each stamen is terminated by an ovate membranaceous appendage, sagittate at the base.

GEOGRAPHICAL DISTRIBUTION

The genus *Echinacea* has its center of development in the prairies and glades of the central United States, including the region from Illinois to Iowa, south to Tennessee and Oklahoma. The species are usually inhabitants of dry, rocky glades, with a preference for limestone soils. *Echinacea purpurea* has the widest distribution, its range extending from Georgia, north and west to Kentucky and the Ozarkian region of Missouri and Arkansas. The remaining species are less widely distributed; for example, in the region east of the Mississippi River, *E. laevigata* occurs along the Appalachian Upland east of the Alleghenies from Pennsylvania to Georgia. A more restricted range is found in *E. angustifolia* var. *tennesseensis*, which is known only from the dry, rocky hills or pine barrens of Rutherford County, Tennessee. *Echinacea pallida* is an inhabitant of the prairies and glades of the central United States, and extends into Oklahoma and Texas. *Echinacea paradoxa* is an Ozarkian species extending from southwestern Missouri to Texas, while *E. angustifolia* is confined to the dry prairies and barrens ranging from northern Minnesota to Texas.

Economic Uses.—*Echinacea* is at present of little importance in an economic way. The main value lies in horticultural possibilities. The New Colwall Strain of *Echinacea purpurea* has been recently placed on the market in England. It is of easy culture, quite hardy, and the handsome heads are often six inches in diameter. The most beautiful part of the head is the cone center which is green or bronze when young and later becomes gorgeously tinted with metallic shades of copper, bright brown, or red. Other species of this genus also make attractive border plants.

TAXONOMY

Echinacea Moench, Meth. Pl. 591. 1794; Less. Syn. Gen. Comp. 225. 1832; DC. Prodr. **5**: 554. 1836; Endl. Gen. Pl. 409. 1838; Meisner, Pl. Vasc. Gen. 202. 1839; Endl. Ench. Bot. 238. 1841; Torr. & Gray, Fl. N. Am. **2**: 305. 1842; Lemaire in Dict. Hist. Nat. 183–184. 1844; Benth. & Hook. Gen. Pl. **2**: 366. 1873; Gray, Syn. Fl. N. Am. **1**^{2}: 258. 1884.

Dracunculus Morison, Pl. Hist. pt. 3. sect. 6. 42, *pl. 9*. 1699.

Bobartia Petiver, Herbal, 473. [1715]. 1704.

Brauneria Necker, Elem. Bot. **1**: 17. 1790.

Helichroa Raf. Neogenyton, 3. 1825.

Herbaceous perennials, arising from vertical or horizontal rootstalks. Stems erect, simple or branched, smooth to variously pubescent. Leaves alternate, ovate, ovate-lanceolate to lanceolate, acute or attenuated, coarsely toothed or entire, dark or light green, smooth or pubescent, 3–5-veined, medium in texture. Involucral bracts 2–3-seriate, foliaceous, linear-lanceolate to lanceolate, attenuate or acute, ciliate, smooth or pubescent, of medium texture. Receptacle distinctly conical. Pales conduplicate, terminating in sharp cartilaginous spines, exceeding the disk-flowers, straight or somewhat incurved. Ray-flowers neutral, disposed in one series, rays strap-shaped, bifid or trifid, purple or occasionally yellow. Disk-flowers fertile. Disk-corollas expanded below into a bulb-like base and sessile upon the achene, contracted above into a cylindrical tube and the five-lobed erect limb, smooth, purplish. Stamens five, anthers sagittate at the base, terminating in an ovate,

membranaceous appendage. Styles usually enlarged slightly at the base, equalling or slightly shorter than the corolla, the branches acuminate, hairy. Achenes four-angled, in cross-section diamond-shaped at top, smooth, often sparsely pubescent on the angles, terminated by a toothed crown, body of the achene usually glabrous, slightly areolated.

Type species: *E. purpurea* Moench, Meth. Pl. 591. 1794.

KEY TO THE SPECIES

A. Leaves ovate to ovate-lanceolate; pales slender, terminating in long weak spines.

B. Stem and leaves hirsute, not glaucous.......................*1. E. purpurea*

BB. Stem and leaves smooth or glaucous.......................*2. E. laevigata*

AA. Leaves lanceolate, attenuate at each end; pales stout, terminating in stiff spines.

C. Plants hirsute or tuberculate-hirsute; stem and leaves dark green; rays purple.

D. Stem and leaves tuberculate-hirsute to tuberculate-hispid; rays 2–3.5 cm. long, not reflexed.............................*3. E. angustifolia*

DD. Stem and leaves hirsute; rays 4–9 cm. long, reflexed........*4. E. pallida*

CC. Plants strigose; stem and leaves light green; rays yellow....*5. E. paradoxa*

1. **Echinacea purpurea** Moench, Meth. Pl. 591. 1794; DC. Prodr. **5**: 554. 1836; Spach, Hist. Nat. Veg. **10**: 52. 1841; Torr. & Gray, Fl. N. Am. **2**: 305. 1842; Gray, Syn. Fl. N. Am. **1**^{2}: 258. 1884; Chapm., Fl. Southern U. S., ed. 3, 248. 1897; Britt. & Brown, Ill. Fl. ed. 2, **3**: 475, *fig. 4456.* 1913; Rydb. Fl. Cent. N. Am. 837. 1932; Small, Man. Southeast. Fl. 1421. 1933.

Rudbeckia purpurea L. Sp. Pl. **2**: 907. 1753; Walt. Fl. Car. 214. 1788; Michx. Fl. Bor.-Am. **2**: 143. 1803; Nutt. Gen. N. Am. Pl. 178. 1818; Link, Enum. Pl. 353. 1821; Barton, Fl. N. Am. **2**: 84, *pl. 64.* 1822; Elliot, Sketch Bot. Car. & Ga. **2**: 449. 1824.

Chrysanthemum americanum Pluk. Alm. Bot. 99. 1696; *ibid. pl. 21. fig. 1.* 1720.

Dracunculus Virginianus latifolius Morison, Pl. Hist. pt. 3. sect. 6. 42, *pl. 9.* 1699.

Rudbeckia serotina Sweet, Brit. Fl. Gard. **1**: *pl. 4.* 1823–25.

Echinacea intermedia Lindl. in Paxt. Mag. Bot. **15**: 79. 1849.

Brauneria purpurea (L.) Britt. Mem. Torr. Bot. Club **5**: 334. 1893; Britt. & Brown, Ill. Fl. ed. 1, **3**: 420, *fig. 3895.* 1898;

Small, Fl. Southeast. U. S. ed. 1, 1261. 1903, and ed. 2, 1261. 1913; Rob. & Fern. in Gray's Manual, ed. 7, 832. 1908.

Stems erect, stout, branched, hirsute below, becoming smooth above, 6–18 dm. high; leaves ovate to ovate-lanceolate, acute, coarsely or sharply serrate below, usually entire above, hirsute on both surfaces, mature leaves often rough to the touch, 3–5-veined; basal leaves long-petiolate, 1.7–4.7 dm. long, 6–9 cm. broad; cauline leaves short-petiolate, sessile above, 7–19 cm. long, 1.5–7 cm. broad; involucral bracts linear-lanceolate, attenuate, entire, ciliate, pubescent on outer surface, texture similar to the leaf; heads 1.5–2.7 cm. high, 1.1–4 cm. broad exclusive of the rays; pales slender, lanceolate, 11–13 mm. long, 1–1.5 mm. broad, terminating in long spines, surpassing the corolla 5–6 mm., smooth, purplish to brownish; rays 4–5.5 cm. long, 5–10 mm. broad, bidentate or entire, reddish-purple; achenes 4–4.5 mm. long, 2–3 mm. broad at top, glabrous.

Distribution: prairies and dry open woods from Ohio to Georgia, west to Iowa and Arkansas.

GEORGIA: dry soil, Gwinnett Co., July 7, 1897, *Eggert* (M); "Griers Fave," Randolph Co., July 17, 1903, *Harper 1884* (M).

OHIO: Mineral Springs, Adams Co., Oct. 5, 1930, *Stephenson* (M).

TENNESSEE: Cumberland Mt., Franklin Co., July 21, 1897, *Eggert* (M); Cumberland Mts., Cowan, July, 1898, *Ruth 646* (M); Wolf Creek, July 28, 1894, *Kearney* (M).

ALABAMA: Chambers Co., June 21, 1897, *Earle* (M).

ILLINOIS: Wady Petra, Stark Co., July 19, 1900, *Chase 685* (M); Hancock Co., *Meade 1841* (M).

MISSOURI: Webster, St. Louis Co., July 27, 1898, *Brownell* (M); Shell Mound, Barry Co., July 11, 1927, *Palmer 32445* (M); near St. Louis, St. Louis Co., Aug. 4, 1892, *Glatfelter 275* (M); Windsor Springs, July 28, 1891, *Douglas* (M); Eureka Springs, July 16, 1898, *Glatfelter* (M); Oakville, Jefferson Co., Sept. 1, 1926, *Mathias* (M); Dasco, Ralls Co., Aug. 13, 1915, *Davis 4864* (M); Hannibal, Marion Co., July 6, 1916, *Davis 1574* (M); Webster Groves, St. Louis Co., Sept., 1920, *Greenman 4007* (M); near Allenton, July 30, 1897, *Letterman* (M); James River, Stone Co., June 3, 1914, *Palmer 5843* (M); Mark Twain's Cave, Marion Co., Aug. 24, 1915, *Davis 3284* (M); Arcadia, Iron Co., Sept., 1897, *Russell* (M); Pleasant Grove, Ripley Co., July 20, 1897, *Mackenzie 373* (M); McDonald Co., July 24, 1892, *Bush* (M); Silex, Lincoln Co., Sept. 16, 1916, *Davis 1844* (M); Jackson Co., Aug. 28, 1884, *Bush* (M); Eagle Rock, Barry Co., June 8, 1897, *Bush 26* (M); Noel, McDonald Co., Sept. 10, 1913, *Palmer 42569* (M); Spring Park, July 24, 1891, *Hassford* (M); Oak Grove, Jackson Co., July 30, 1902, *Mackenzie 64* (M); Monteer, Aug. 8, 1910, *Bush 6146* (M); river bluffs, near Hannibal, Marion Co., Jan. 9, 1915, *Davis 5819* (M).

ARKANSAS: Eureka Springs, July 16, 1898, *Glatfelter* (M); Benton Co., *Plank* (M); Fulton, Hempstead Co., June 19, 1915, *Palmer 8040* (M).

2. **Echinacea laevigata** (Boynton & Beadle) Blake in Jour. Wash. Acad. Sci. **19**: 273. 1929; Small, Man. Southeast. Fl. 1421. 1933.

Brauneria laevigata Boynton & Beadle in Small, Fl. Southeast. U. S. ed. 1, 1261. 1903, and ed. 2, 1261. 1913.

Stems erect, simple or branched, glabrous, striate, 9–12 dm. high; leaves glabrous on both surfaces, palmately 3–5-veined, medium in texture; basal leaves long-petiolate, 18–36 cm. long, 3–7 cm. broad, cauline short-petiolate below, sessile above, ovate to broadly lanceolate, acute, finely serrate, 7–18 cm. long, 2–5 cm. broad; heads 2–2.5 cm. high, 3–3.5 cm. broad exclusive of the rays, pales slender, linear-lanceolate, 9 mm. long, 1 mm. broad, tips curving inwards, surpassing the corolla; rays 3.5–8 cm. long, 3–5 mm. broad, reflexed bidentate, purple; disk-corolla 5 mm. long, purplish; achenes 4 mm. long, glabrous, somewhat areolated, pappus a toothed crown of equal length.

Distribution: fields and woods, Lancaster Co., Pennsylvania, south to South Carolina and Georgia.

PENNSYLVANIA: Lancaster Co., "Caernavron" township, July, *without collector* (M).

VIRGINIA: Bradford Co., July 18, 1871, *Curtiss 3502* (M); near Staunton, Augusta Co., June 18, 1896, *Murrill* (NY).

SOUTH CAROLINA: Keowee, Oconee Co., May 22, 1906, *House 2206* (M).

GEORGIA: in mountains of Georgia, *Buckley* (M).

3. **Echinacea angustifolia** DC. Prodr. **5**: 554. 1836; Torr. & Gray, Fl. N. Am. **2**: 306. 1842; Gray, Syn. Fl. N. Am. **1**[2]: 258. 1884; Britt. & Brown, Ill. Fl. ed. 2, **3**: 476, *fig. 4457*. 1913; Rydb. Fl. Pr. & Pl. Cent. N. Am. 837, *fig. 570*. 1932.

Brauneria angustifolia (DC.) Heller in Muhlenbergia **1**: 5. 1900; Small, Fl. Southeast. U. S. ed. 1, 1261. 1903, and ed. 2, 1261. 1913; Rob. & Fernald in Gray's Manual, ed. 7, 832. 1908; Rydb. Fl. Rocky Mts. ed. 1, 926. 1917, and ed. 2, 926. 1922.

Echinacea sanguinea Nutt. in Trans. Am. Phil. Soc. II. **7**: 354. 1841.

Stems simple, 3–5 dm. high, tuberculate-hirsute to tuberculate-hispid; leaves oblong-lanceolate to long-elliptical, entire,

dark green, tuberculate-hirsute to tuberculate-hispid, rough to the touch; basal leaves long-petiolate, 9–22 cm. long, 1–2.5 cm. broad, cauline sessile, 4–14 cm. long, .6–1.5 cm. broad, acute; heads 1.9–3 cm. high, 1.5–2.5 cm. broad exclusive of the rays, involucral bracts lanceolate, acute, entire, 6–11 mm. long, 2–3 mm. wide, densely tuberculate-hirsute or tuberculate-hispid; rays spreading, sparsely pubescent on the veins below, 2–3.5 cm. long, 3–8 mm. broad, once- or twice-notched, purplish; disk-corollas 6–7 mm. long, purplish; achenes 5 mm. long, main body areolated by light brown and dark brown splotches, pappus forming a toothed crown.

Distribution: dry prairies and barrens, Minnesota, south to Texas, west to Wyoming.

MINNESOTA: Pike Lake, Sept. 10, 1849, *Sykes* (M).

NORTH DAKOTA: Minot, Ward Co., Aug. 3, 1928, *Larsen 198* (M).

SOUTH DAKOTA: Brookings, Brookings Co., without date, *Williams* (M); Deadwood, Lawrence Co., July 14, 1913, *Carr 90* (M); Ionia, Lyman Co., July 5, 1910, *Rose* (M); Iriquois, Kingsbury Co., Aug. 9, 1894, *Thornber* (M); Forestburg, Sanborn Co., July 3, 1910, *Visher 4454* (M); near Hot Springs, Fall River Co., June 27, 1929, *Palmer 37546* (M).

NEBRASKA: without locality, July, 1904, *Goodding 2215* (M); Lincoln, Lancaster Co., June, 1886, *Webber* (M).

KANSAS: Ellis Co., 1908–11, *Zeller* (M); Manhattan, Riley Co., July 12, 1892, *Clothier* (M); prairie, June 18, 1895, *Norton 265* (M); Rockport, Rooks Co., June 26, 1889, *Bartholomew* (M); east of Russell, Russell Co., July 1, 1926, *Heller 13984* (M); Fort Kearney, July 10, 1856, *Engelmann* (M).

OKLAHOMA: Cache, Comanche Co., June 25, 1913, *Stevens 1341K* (M); near Fort Sill, June 14, 1916, *Clemens 11837* (M); near Cora, Woods Co., May 28, 1913, *Stevens 737* (M); near Rocky, Washita Co., June 16, 1913, *Stevens 971* (M).

TEXAS: near Canyon City, Randall Co., Aug. 14, 1900, *Eggert* (M); Dallas, Dallas Co., June 15, 1898, *Glatfelter* (M); Comanche Spring, Comanche Co., May, 1849, *Lindheimer 898* (M); Kerrville, Kerr Co., May 7–14, 1894, *Heller 1735* (M); Leon Springs, Bexar Co., *Clemens & Clemens 381* (M).

WYOMING: Lake De Smet, July 30, 1901, *Nelson 8546* (M); Sundance, Crook Co., July 21, 1896, *Nelson 2122* (M); Dome Lake, Sheridan Co., June 27, 1897, *Pammel & Stanton 247* (M).

3a. var. **tennesseensis** (Beadle) Blake in Jour. Wash. Acad. Sci. **19**: 273. 1929.

Brauneria tennesseensis Beadle in Bot. Gaz. **25**: 359. 1898; Small, Fl. Southeast. U. S. ed. 1, 1262. 1903, and ed. 2, 1262. 1913.

Echinacea tennesseensis (Beadle) Small, Man. Southeast. Fl. 1421. 1933.

Stems usually simple, 1–4.5 dm. high, hirsute or tuberculate-hirsute; leaves narrowly oblong or long-elliptical, acute, entire, 2–13 cm. long, 3–7 mm. broad, hirsute, often tuberculate-hirsute, short-petiolate below, sessile above; involucral bracts linear, 5–7 mm. long, 2 mm. broad, hirsute-ciliate; achenes 4.5–5 mm. long, glabrous.

Distribution: pine barrens and dry hills, Tennessee.

TENNESSEE: Lavergne, Rutherford Co., July 14–Aug. 18, 1897, *Eggert* (M); Lavergne, Sept. 7, 1898, *Eggert* (M); same locality, Aug. 19, 1897, *Biltmore Herb. 1107* (M); cedar barrens, "middle" Tennessee, July 18–19, *Gattinger* (M).

4. **Echinacea pallida** Nutt. in Trans. Am. Phil. Soc. II. **7**: 354. 1841; Britt. & Brown, Ill. Fl. ed. 2, **3**: 476, *fig. 4458.* 1913; Rydb. Fl. Pr. & Pl. Cent. N. Am. 837. 1932; Small, Man. Southeast. Fl. 1421. 1933.

Echinacea angustifolia Hook. in Curt. Bot. Mag. **17**: *pl. 5281.* 1861, not DC.

Rudbeckia pallida Nutt. in Jour. Acad. Nat. Sci. Phila. **7**: 17. 1834.

Brauneria pallida Britt. in Mem. Torr. Bot. Club **5**: 333. 1894; Britt. & Brown, Ill. Fl. ed. 1, **3**: 420, *fig. 3895.* 1898; Small, Fl. Southeast. U. S. ed. 1, 1261. 1903, and ed. 2, 1261. 1913; Rob. & Fern. in Gray's Manual, ed. 7, 832. 1908.

Stems usually simple, 6–9 dm. high, sparsely hirsute below, more densely so above, pedicels leafless, becoming somewhat enlarged or flattened near the head; leaves oblong-lanceolate to long-elliptical, entire, dark green, hirsute on both surfaces, triple-veined, medium in texture; basal leaves 1.8–3.1 dm. long, 1–3.5 cm. broad, the cauline 10–27 cm. long, 1–2.5 cm. broad, acute; involucral bracts lanceolate or narrowly oblong, 8–17 mm. long, 2.5–4 mm. broad, strongly ciliate, hirsute, often gradually passing into the echinaceous pales; rays strongly reflexed, 4–9 cm. long, 5–8 mm. broad, bidentate, purplish; achenes 4 mm. long, glabrous, pappus a toothed crown.

Distribution: dry prairies and barrens, Illinois and Kentucky west to Nebraska, southwest to Texas.

ILLINOIS: Peoria, Peoria Co., June 10, 1912, *Churchill* (M); near Wady Petra, Stark Co., June 25, 1900, *Chase 642* (M); near French Village, St. Clair Co., June 15, 1876, *Eggert* (M).

KENTUCKY: Bowling Green, Warren Co., Aug., 1890, *Price* (M).

IOWA: Iowa City, Johnson Co., *Hitchcock* (M); Columbus Junction, Louisa Co., June, 1925, *Graves* (M); Black Hawk Co., June 18, 1929, *Burk 772* (M); ledges, State Park, Boone Co., June 30, 1926, *Pammel 243* (M).

MISSOURI: Oakwood, Ralls Co., June 21, 1916, *Davis 4185* (M); Winfield, Lincoln Co., June 7, 1916, *Davis 4405* (M); Allenton, St. Louis Co., May 20, 1895, *Letterman* (M); Eureka, May 30, 1900, *Norton* (M); Benton, June 21, 1885, *Wislizenus 196* (M); Pacific, Franklin Co., June 3, 1918, *Greenman 4121* (M); Gray's Summit, Franklin Co., May 25, 1927, *Kellogg* (M); Jefferson Co., May 25, 1896, *Eggert* (M); Potosi, Washington Co., June 6, 1892, *Dewart* (M); Ironton, Iron Co., June 26, 1920, *Palmer 18088* (M); Jerome, Phelps Co., June 1, 1914, *Kellogg 438* (M); Cape Girardeau, Cape Girardeau Co., June 22, 1920, *Palmer 18016* (M); Gainesville, Ozark Co., June 26, 1928, *Palmer 34749* (M); Swan, Taney Co., June 10, 1898, *Bush 149* (M); Galena, Stone Co., May 28, 1914, *Palmer 5783* (M); Eagle Rock, Barry Co., May 26, 1898, *Bush 261* (M); Webb City, Jasper Co., June 22, 1902, *Palmer 178* (M); Nichols' Junction, Greene Co., June 15, 1898, *Bush 38* (M); Sheffield, Jackson Co., June 26, 1894, *Bush 156* (M).

ARKANSAS: near Mandelville, Miller Co., June 10, 1898, *Eggert* (M); near Texarkana, June 8, 1898, *Eggert* (M); Fulton, Hempstead Co., June 19, 1915, *Palmer 8061* (M).

LOUISIANA: Jennings, Jefferson Davis Parish, May 15, 1915, *Palmer 7632* (M).

NEBRASKA: Lincoln, Lancaster Co., June 11, 1900, *Hedgcock* (M).

KANSAS: Cowley Co., June, 1898, *White* (M); Caney, Montgomery Co., June 29, 1929, *Rydberg & Imler 400* (M).

OKLAHOMA: Page, Leflore Co., June 20, 1914, *Blakley 1436* (M).

TEXAS: Willis, Montgomery Co., June, *Warner* (M); Houston, Harris Co., June 2, 1915, *Fisher* (M); near Buchanan, Bowie Co., June 13, 1898, *Eggert* (M); Mineola, Wood Co., June, *Reverchon 2072* (M); Dallas, Dallas Co., June 26, 1899, *Eggert* (M); Big Sandy, Upshur Co., May 28, 1900, *Reverchon 2579* (M); Hempstead, Waller Co., June 10, 1872, *Hall 330* (M); Weatherford, Parker Co., May 29, 1902, *Tracy 8331* (M); Grapeland, Houston Co., May 26, 1917, *Palmer 12066* (M); Gladwater, Gregg Co., June, *Reverchon* (M); Boerne, Kendall Co., May 22, 1916, *Palmer 9853* (M).

5. **Echinacea paradoxa** (Nort.) Britt. & Brown, Ill. Fl. ed. 2, 3: 476, *fig. 4459.* 1913.

Brauneria paradoxa Norton in Trans. Acad. Sci. St. Louis 12: 40. 1902; Rob. & Fern. in Gray's Manual, ed. 7, 832. 1908; Small, Fl. Southeast. U. S. ed. 1, 1261. 1903, and ed. 2, 1261. 1913.

Stems simple, 3.5–8.5 dm. high, stramineous or yellowish-green, sparsely or densely strigose, sometimes tuberculate-

strigose on the peduncles; leaves oblong-lanceolate to long-elliptical, entire, light green, strigose-pubescent on both surfaces, more densely so below, medium in texture; basal leaves long-petiolate, 1–2.5 dm. long, 1–3.2 cm. broad, the cauline .6–3 dm. long, .5–2.5 cm. broad, acute; involucral bracts 7–10 mm. long, 1–4 mm. broad, lanceolate, acute, the outer foliaceous, the inner passing into the pales, smooth, strigose-ciliate; rays 3–7 cm. long, 3–8 mm. broad, yellow; achenes 4–5 mm. high, glabrous, teeth of the pappus-crown equal in length.

Distribution: rocky slopes and barrens, Missouri to Texas.

MISSOURI: Nichols' Junction, Greene Co., June 15, 1898, *Bush 42* (M); James River, Stone Co., June 3, 1914, *Palmer 5844* (M); Swan, Taney Co., June 10, 1898, *Bush 155* (M); near Seligman, Barry Co., June 1, 1926, *Palmer 30397* (M); Eagle Rock, Barry Co., June 4, 1897, *Bush 76* (M); near Gainesville, Ozark Co., June 26, 1928, *Palmer 34714* (M).

OKLAHOMA: Idabel, McCurtain Co., May 18, 1916, *Houghton 3642* (M).

TEXAS: Willis, Montgomery Co., *Warner* (M); Houston, Harris Co., April 29, 1916, *Palmer 9617* (M); Valley of the Trinity River, June 28, 1912, *Bush 243* (M).

ZALUZANIA Pers.

History.—The genus *Zaluzania* was first published by Persoon[1] in 'Synopsis Plantarum' in 1807; it was based on *Anthemis triloba* Ort., a plant native of Mexico.

Lagasca,[2] in 'Genera et Species Plantarum' in 1816, described the genus *Ferdinanda* and included two species, *F. augusta,* now *Zaluzania augusta,* and *F. eminens,* now *Podachaenium paniculatum* Benth. Cassini,[3] Kunth,[4] DeCandolle,[5] and Endlicher[6] recognized Lagasca's genus in their treatment of the Heliantheae. The generic limitations of *Ferdinanda* were rather broad and included species with or without a pappus, etc., the pappose species now being included in *Podachaenium. Chrysophania* of Kunth[4] is synonymous wth *Ferdinanda,* since its type species *C. fastigiata* is a synonym of *Zaluzania*

[1] Persoon, C. H., Syn. Pl. 2: 473. 1807.
[2] Lagasca, A. M., Gen. et Sp. Nov. Pl. 31. 1816.
[3] Cassini, M. H., in Dict. Sci. Nat. 46: 404. 1827.
[4] Kunth, C., in Less. Syn. Gen. Comp. 224. 1832.
[5] De Candolle, A., in DC. Prodr. 5: 552. 1836.
[6] Endlicher, S., Gen. Pl. 408. 1838.

augusta, the species on which *Ferdinanda* was based. Robinson and Greenman[7] in 1899 treated *Ferdinanda* as a subgenus under *Zaluzania.* This position is retained in the present revision of this genus.

Hybridella was described briefly by Cassini[8] in 'Bulletin des Sciences, par la Societe Philomatique' in 1817, and was based on *Anthemis globosa* Ort. *Hybridella* was never recognized as a genus by other authors. Robinson & Greenman[7] in 'Proceedings of the American Academy' in 1899 treated it as a subgenus under *Zaluzania,* this disposition being retained in the present paper. It comprises those palustrine, herbaceous species of *Zaluzania* with finely dissected leaves. *Chilophyllum* of De Candolle[9] described in the "Prodromus" in 1836 is synonymous with *Hybridella.*

A taxonomic study of *Zaluzania* was published by Schultz-Bipontinus in "Flora" in 1861[10] and 1864.[11] His treatise of 1861 comprised seven species, three of which were new, namely, *Z. megacephala, Z. montagnaefolia,* and *Z. myriophylla.* His publication on the genus in 'Flora,' 1864, included twelve species, eight of which belong to *Zaluzania,* three have been transferred to *Viguiera,* and one to *Calea.*

Between 1864 and 1898 four new species were added to *Zaluzania,* namely, *Z. mollissima, Z. Coulteri, Z. resinosa,* and *Z. discoidea.* The genus now totalled eleven species, all native of Mexico, *Zaluzania Coulteri* having been found to be synonymous with *Z. cinerascens.* The first comprehensive revision of the genus by Robinson and Greenman[7] in 'Proceedings of the American Academy' in 1899 added two new species. The genus, at this time, was known only from Mexico and Arizona.

Hieronymus[12] in Engler's 'Botanische Jahrbücher' in 1900 described three new species from Ecuador. This is the only record of *Zaluzania* from South America; and of these three

[7] Robinson, B. L., and Greenman, J. M., in Proc. Am. Acad. Sci. **34**: 531–534. 1899.

[8] Cassini, M. H., in Bull. Soc. Philom. p. 12. 1817.

[9] De Candolle, A., in Prodr. **5**: 554. 1836.

[10] Schultz-Bipontinus, C. H., in Flora **44**: 561–565. 1861.

[11] Schultz-Bipontinus, C. H., in Flora **47**: 216–220. 1864.

[12] Hieronymus, G., in Engl. Bot. Jahrb. **29**: 35–37. 1900.

species *Z. Sodiroi* is the only one retained in the present monograph; the other two pass into synonymy.

GENERAL MORPHOLOGY

Roots.—The roots of the various suffruticose and shrubby species of the genus are little known, because, due to their bulk, they have not been taken by collectors. This also may apply to the herbaceous species that attain a height of three feet or more. The roots are mostly biennial or perennial in all the species of *Zaluzania*. In *Z. globosa* and its variety the main root is relatively short and rhizome-like with numerous secondary fibrous roots. *Zaluzania Grayana* is the only species known to the author that possesses a thickened tuberous rootstalk surmounted by a slender, lignescent, branched base which gives rise to the suffrutescent stems.

Stems.—The stems of *Zaluzania* are terete and usually more or less striated. They vary from herbaceous to lignescent. The herbaceous type is especially exemplified in *Z. globosa, Z. anthemidifolia, Z. triloba, Z. discoidea,* and *Z. megacephala.* The suffruticose forms are lignescent at their base or upwards for half the height of the plant, the flower-bearing branches being herbaceous. This type may be observed in *Z. Robinsonii* and *Z. Grayana.* The shrubby species are especially exemplified by *Z. Pringlei* and *Z. montagnaefolia.*

Leaves.—Two quite different forms of leaves are displayed in the genus, namely, (1) finely dissected leaves, and (2) undivided or lobed leaves. The former group, comprising species that inhabit moist or swampy localities, as *Z. globosa* and its variety *myriophylla,* often have leaf-segments 3–4-pinnatisect.

The second group is typified by the subgenus Ferdinanda. Three species, namely, *Z. Grayana, Z. triloba,* and *Z. Robinsonii,* have pinnately, or more commonly palmately, lobed leaves. The remaining species display undivided leaves which are ovate, ovate-lanceolate to ovate-elliptical in outline, acute to broadly obtuse, and entire to variously dentate or serrate. The venation is chiefly of the pinnate type, usually with three prominent veins near the base of the leaf. Leaves with pro-

nounced reticulations are exemplified in *Z. Sodiroi,* and to a less degree in *Z. montagnaefolia.*

Pubescence.—The common type of pubescence in *Zaluzania* consists of simple unbranched hairs. The species are all more or less pubescent, except *Z. anthemidifolia,* which is glabrous. The degree and character of this covering vary with the different species. The hirsute type is less common, *Z. globosa* and *Z. triloba* being the best examples. The softer types of trichomes, varying from crispy hirtellous, velutinous, to velvety tomentose, are the most common forms within the genus. The velutinous or velvety tomentose type of pubescence is shown in *Z. augusta, Z. subcordata, Z. mollissima,* and *Z. discoidea.* Short-stiped or sessile, globular, resinous glands are present in the majority of the species.

Inflorescence.—The corymbose to subpaniculate types of inflorescence are dominant for *Zaluzania.* The Hybridella section has a tendency towards the production of heads in very loose panicles, or solitary, as in *Z. anthemidifolia.* The inflorescence is of little significance in separating the species.

The receptacle is conical with persistent pales. The pales are of two sorts, namely, the linear, plane, herbaceous type characteristic of Hybridella, and (2) the complicate or boat-shaped subcoriaceous type as in the subgenus Ferdinanda. The pales are of little importance for specific delimitation but they serve as important subgeneric characters.

Corollas.—All the species of *Zaluzania,* with the exception of *Z. discoidea* and *Z. Pringlei,* have heterogamous flower-heads, with styliferous and fertile ray-flowers, and fertile, tubular disk-florets. The corollas are yellow in both ray- and disk-flowers. The ligules are ovate, oblong-ovate, to oblong, 2–3-denticulate or subentire, always styliferous. The tube in some species is dilated at the base so as to completely cap the achene. The disk-corollas have a narrow cylindrical tube which is about half the length of the corolla proper, and always expanded at the base so as to cap the achene; the throat is campanulate, glabrous or pubescent, with a somewhat spreading five-lobed limb. The expanded base of the corolla and the fer-

tile ray-flowers constitute the major characters of generic importance.

The androecium is composed of five syngenesious stamens with ovate appendages and sagittate bases, which are similar to those of related genera. The style-branches are slender, more or less recurved, with acute or obtuse appendages. Their apices are variously pubescent.

Achenes and Pappus.—The achenes of the disk-flowers are ordinarily linear-cuneate or narrowly oblong and somewhat four-angled; the ray-achenes are triangulate. The disk-achenes are glabrous, the ray-achenes variously pubescent or glabrous. The variation of the achenes within the genus is very slight and consequently of no specific importance. The disk-achenes are devoid of a pappus. The ray-achenes are epappose or crowned by a pappus varying from short-hirsute hairs to fimbriate or squamulose setae.

Geographical Distribution.—The center of distribution for this genus is in the Mexican Plateau. *Zaluzania Grayana* is the most northerly distributed species; it occurs in the mountains of Chihuahua and southern Arizona. The most extra-limital species is *Z. Sodiroi,* known to occur only in the mountains of Ecuador, South America. Five of the fourteen species included in this genus have a limited distribution; for example, *Z. anthemidifolia* is known only from Jalisco; *Z. Pringlei* inhabits limestone hills near Jojutla in the state of Morelos; *Z. cinerascens* is known to occur only among the fir forests of the Sierra Pachuca Mountains in the state of Hidalgo; *Z. megacephala* is found in the mountains of Coahuila at an elevation of 6500–10,000 feet; whereas *Z. subcordata* is an inhabitant of the dry, rocky or barren hills and mountains of southeastern Puebla. *Zaluzania discoidea* and *Z. montagnaefolia* are known to occur only in two states of Mexico; the former inhabits the dry, rocky hills and mountains of Chihuahua and Durango, whereas the latter occupies a similar habitat in the states of Puebla and Oaxaca. The remaining five species occur in central Mexico with a general range from Durango south to the states of Mexico and Hidalgo.

The species of the subgenus Hybridella occur at relatively lower altitudes in palustrine or moist habitats. The species assigned to the subgenus Ferdinanda occur at high altitudes, ranging usually from 5000 to 10,000 feet elevations.

TAXONOMY

Zaluzania Pers. Syn. Pl. **2**: 473. 1807; Less. Syn. Gen. Comp. 224. 1832; DC. Prodr. **5**: 553. 1836; Endl. Gen. Pl. 408. 1838; Walp. Rep. Bot. Syst. **2**: 611. 1843; Schz.-Bip. in Flora **44**: 561–565. 1861; *Ibid.* **47**: 216. 1864; Benth. & Hook. Gen. Pl. **2**: 362. 1873; Hemsl. Biol. Cent.-Am. Bot. **2**: 159. 1881; Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. IV. Abt. 5: 233. 1890; Rob. & Greenm. in Proc. Am. Acad. **34**: 530. 1899; Blake in Contr. U. S. Nat. Herb. [Standley's Trees & Shrubs Mexico] **23**: 1537. 1926.

Ferdinanda Lag. Gen. & Sp. Nov. Pl. 31. 1816; Cass. in Dict. Sci. Nat. **46**: 404. 1827; Kunth in Less. Syn. Gen. Comp. 224. 1832; DC. Prodr. **5**: 552. 1836; Endl. Gen. Pl. 408. 1838.

Hybridella Cass. in Bull. Soc. Philom. 12. 1817; in Dict. Sci. Nat. **22**: 86. 1821.

Chrysophania Kunth in Less. Syn. Gen. Comp. 224. 1832; DC. Prodr. **5**: 553. 1836; Endl. Gen. Pl. 408. 1838.

Chiliophyllum DC. Prodr. **5**: 554. 1836, not *Chiliophyllum* Phil. in Linnaea **33**: 132. 1864; Endl. Gen. Pl. 408. 1838.

Perennial herbs or shrubs, often striated, glabrate, velutinous, tomentulose, or hirsute. Leaves alternate, simple, palmately or pinnately lobed to pinnatisect, entire, serrate to dentate-mucronate, hirsute, strigose-villous, tomentulose to velutinous, frequently interspersed by resinous glands. Heads radiate or discoid, in corymbose, subcorymbose, or subpaniculate clusters, hemispherical to subglobose. Involucre campanulate to subcampanulate, 2–4-seriate, graduated or subequal, the outer bracts sometimes much longer than the inner, ovate, ovate-lanceolate to oblong-lanceolate, herbaceous, the inner series becoming subcoriaceous. Receptacle conical, about 3 mm. high; pales subherbaceous to coriaceous, trilobed or acute at the apex, plane to conduplicate, not deciduous with the achenes. Disk-corollas with the base dilated and capping the

crown of the achene, the tube narrowly cylindrical, expanding above into the campanulate throat and the 5-lobed, spreading or reflexed limb, tube pubescent or glabrous. Stamens sagittate at the base, appendages ovate; style-branches more or less recurved, with obtuse or acute appendages, pubescent at the apex. Ray-corollas yellow, styliferous, the tube often capping the ray-achene. Achenes of the disk-flowers quadrangulate-obcompressed or rhomboidal in cross-section, glabrous, those of the ray-flowers trigonal, glabrous or pubescent; pappus absent in the disk-achenes, absent or consisting of minute fimbriate or squamellose setae in the ray-achenes.

Type species: *Z. triloba* (Ort.) Pers. Syn. Pl. **2**: 473. 1807.

KEY TO THE SUBGENERA

A. Leaves finely pinnatisect; pales linear, plane, herbaceous or subherbaceous; palustrine herbs.......Subgenus Hybridella (Cass.) Rob. & Greenm. Sp. 1–2.

AA. Leaves simple or lobed; pales conduplicate, coriaceous to subcartilaginous; perennial herbs or shrubs of mesophytic or dry habitats.................................Subgenus Ferdinanda (Lag.) Rob. & Greenm. Sp. 3–14.

KEY TO THE SPECIES AND VARIETIES

A. Leaves narrowly pinnately dissected or bipinnatisect; pales linear, plane, herbaceous or subherbaceous.
  B. Leaves finely 2–4-pinnatisect, the ultimate segments less than 1 mm. broad.
    C. Ultimate leaf-segments acute..............................*1. Z. globosa*
    CC. Ultimate leaf-segments obtuse.............*1a. Z. globosa* var. *myriophylla*
  BB. Leaves narrowly pinnate to bipinnate, the ultimate segments 1–2 mm. broad...*2. Z. anthemidifolia*
AA. Leaves undivided or lobed; pales conduplicate, coriaceous or subcoriaceous.
  B. Leaves palmately or pinnately lobed.
    C. Plants hirsute-hispid or densely hirsutulous; heads 8–20 mm. broad including the rays.
      D. Hirsute-hispid; heads 15–20 mm. broad including the rays; leaves bipinnately lobed or cleft; plants herbaceous..............*3. Z. triloba*
      DD. Densely crisp-hirtellous; heads 8–12 mm. broad including the rays; leaves 3-lobed or tripartite; plants suffruticose.........*4. Z. Robinsonii*
    CC. Plants minutely hirtellous to glabrate; heads 20–30 mm. broad including the rays..*5. Z. Grayana*
  BB. Leaves undivided.
      E. Heads discoid.
        F. Plants shrubby; leaves ovate, strigose-puberulent beneath...... ....*6. Z. Pringlei*
        FF. Plants herbaceous from a ligneous base; leaves broadly ovate to deltoid-ovate, velvety tomentose beneath...........*7. Z. discoidea*

EE. Heads radiate.
G. Leaves entire, serrate to crenate-serrate; plants of Mexico.
H. Leaves pustulate-hirsute to pustulate-hispidulous above, crenate-serrate, base decurrent and auriculate *8. Z. montagnaefolia*
HH. Leaves tomentose, velutinous or hirsutulous, base not auriculate.
I. Plants herbaceous or suffruticose, unbranched except in the inflorescence; pappus absent on the ray-achenes.
J. Leaves broadly ovate to ovate-elliptical, 1½ times as long as broad, hirtellous................*9. Z. cinerascens*
JJ. Leaves lanceolate or ovate-lanceolate, about three times as long as broad, velutinous..........*10. Z. megacephala*
II. Plants shrubby, freely branched below; pappus of the ray-achenes a crown of minute lacerate or squamose setae.
K. Heads including the rays 2–3 cm. broad, rays 1–1.5 cm. long; leaf-blades attenuately decurrent to the base of the petiole...............*11. Z. mollissima*
KK. Heads including the rays less than 1.5 cm. broad, rays 5–8 mm. long; leaf-blades subcordate, not decurrent to the base of the petiole.
L. Leaves entire, subcordate, densely tomentose beneath...........................*12. Z. subcordata*
LL. Leaves below the branches of the inflorescence crenate-serrate to coarsely serrate, velutinous beneath.............................*13. Z. augusta*
GG. Leaves mucronate-dentate; plants of South America.*14. Z. Sodiroi*

1. **Zaluzania globosa** (Ort.) Schz.-Bip. in Flora **44**: 564. 1861; Hemsl. Biol. Cent.-Am. Bot. **2**: 159. 1881; Rob. & Greenm. in Proc. Am. Acad. **34**: 530. 1899.

Anthemis globosa Ort. Desc. Pl. 46. 1797; Jacq. Desc. Rar. Pl. **3**: 64, *pl. 372.* 1798.

Hybridella globosa (Ort.) Cass. in Dict. Sci. Nat. **22**: 86. 1821.

Chiliophyllum globosum (Ort.) DC. Prodr. **5**: 554. 1836; Benth. Pl. Hartweg. 17. 1839.

Perennial palustrine herbs; stems 2–5 dm. tall, slender, sulcate, hirsute to pilose-hirsute, also glandular on the peduncles; basal leaves several, oblanceolate in general outline, finely pinnately dissected, often 3–4-pinnatisect, 1–2 dm. long, 2–4 cm. broad, hirsute to pilose-hirsute, and glandular, segments 2–3 mm. long, linear-lanceolate, acute, the petioles pilose-hirsute; stem-leaves few subtending the pedunculate branches, 2 to 8 on naked pedunculate branches, 2–3 cm. broad including the

rays, 6–10 mm. long; bracts of the involucre herbaceous, lanceolate to oblanceolate, 5–6 mm. long, 1.5–2 mm. broad, hirsute-ciliate, acute, hirsute and more or less glandular; pales weak, almost herbaceous, narrowly linear, 3–4 mm. long, 0.5 mm. or less broad, ciliate, obtuse to acute, glandular on the outer surface; disk-flowers densely glandular on the outer surface of the tube; ray-flowers bidentate, 6–12 mm. long including the achene; mature achenes about 2 mm. long, glabrous, pappus absent.

Distribution: low wet meadows and swampy grounds of central Mexico, San Luis Potosi, southeast to the state of Mexico.

MEXICO: SAN LUIS POTOSI—22° N. lat., alt. 6000–8000 ft., 1878, *Parry & Palmer 527* (M); HIDALGO—Telles, Sept. 21, 1910, *Orcutt 4139* (F, M); Pachuca, July, 1903, *Purpus 77* (M, U CAL, US); MEXICO—wet meadows, Valley of Mexico, alt. 7300 ft., June 7, 1901, *Pringle 9395* (G, M, US); low meadows, Valley of Mexico, Federal District, July 27, 1890, *Pringle 3204* (G, M, U CAL, US); uncultivated fields, Valley of Mexico, June 12, 1865–66, *Bourgeau 385* (G, US); damp meadows, alt. 7300 ft., Valley of Mexico, Federal District, June 25, 1897, *Pringle 7440* (US); Valley of Mexico, June 24, 1889, *Pringle 2925* (G); Valley of Mexico, Aug., 1855, *Schaffner 80* (G); wet meadows, alt. 7300 ft., Tlalnepantla, May 15, 1904, *Pringle 13092* (F, G, US); Valley of Mexico, near Tlalnepantla, June 30, 1901, *Rose & Hay 5274* (US); near Tlalnepantla, July 6, 1905, *Rose, Painter & Rose 8417* (US); Valley of Mexico, near Tacubaya, July 30, 1901, *Rose & Hay 5816* (US).

1a. var. **myriophylla** (Schz.-Bip.) W. M. Sharp, comb. nov.

Zaluzania myriophylla Schz.-Bip. in Flora **44**: 565. 1861; Rob. & Greenm. in Proc. Am. Acad. **34**: 530. 1899.

Zaluzania globosa Schz.-Bip. in Hemsl. Biol. Cent.-Am. Bot. **2**: 159. 1881, in part.

Leaves with the ultimate segments finely dissected, linear, short, 1–2 mm. long, obtuse, hirsute to glabrous; habit and floral characters as in the species.

Distribution: central Mexico, Durango, south to the state of Mexico, inhabiting low wet meadows and swamps.

MEXICO: DURANGO—city of Durango and vicinity, 1896, *Palmer 307* (F, G, M, U CAL, US); ZACATECAS—damp hollows and plains at Colera Station, Sept. 1, 1904, *Pringle 8914* (F, G, M, U CAL, US); SAN LUIS POTOSI—San Luis Potosi, 1879, *Schaffner 770 (345)* (G, US); MEXICO—north of Mexico City, 1837, *Hartweg 111* (G).

The short, linear, obtuse, ultimate segments and the glabrous to sparsely hirsute, glandular leaves warrant at least a varietal

recognition. The ultimate segments of *Z. globosa* are lanceolate, 2–3 mm. long, and acute.

2. **Zaluzania anthemidifolia** Rob. & Greenm. in Proc. Am. Acad. **34**: 531. 1899.

Plants herbaceous; stems decumbent, glabrous; leaves pinnate to bipinnate or bipinnatisect, pilose-hirsute on the midrib and petioles, especially the young leaves, the ultimate segments 1–2 mm. broad, obtusish to acute; heads solitary or sometimes 2 or 3 terminating the leafy branches; peduncles 2–5 cm. long; bracts of the involucre obtuse or obtusish; rays about 1 cm. long, bifid, tube and outer surface of the lamina glandular; disk-corollas with a narrow glandular tube; achenes glabrous; pappus absent.

Distribution: wet sandy banks of the Rio de Santiago River, near Guadalajara, Jalisco.

MEXICO: JALISCO—wet sandy river banks, near Guadalajara, Sept. 23, 1891, *Pringle 5156* (G TYPE); wet sandy banks of the Rio Grande de Santiago, barranca near Guadalajara, Oct. 12, 1895, *Pringle 7367* (F, M, U CAL).

3. **Zaluzania triloba** (Ort.) Pers. Syn. Pl. **2**: 473. 1807; Kunth in Less. Syn. Comp. 225. 1832; DC. Prodr. **5**: 553. 1836; Schz.-Bip. in Flora **44**: 564. 1861; Hemsl. Biol. Cent.-Am. Bot. **2**: 160. 1881; Rob. & Greenm. in Proc. Am. Acad. **34**: 531. 1899.

Anthemis triloba Ort. Desc. Pl. Rar. 72. 1800.

Anthemis trilobata Willd. Sp. Pl. **3**[3]: 2186. 1804.

Anthemis sinuata LaLlave & Lexarza, Nov. Veg. Desc. **1**: 26. 1824.

Herbaceous plants; stems about 6 dm. tall, often irregularly bluish-purple below, branched above, hirsute-hispid; leaves dark green, broadly pinnately parted, including the petiole 2–16 cm. long, 1–5 cm. broad, the segments acute to obtuse, the basal divisions cleft almost to the midrib, the terminal divisions deeply cleft; main cauline leaves long-petiolate, light green beneath and somewhat glandular, densely hirsute-hispid to hirsute especially on the veins, dark green and hirsute-hispid to strigose-hirsute above; inflorescence subcorymbose or subpaniculate; mature heads, including the rays, 1.5–2 cm. broad,

6-10 mm. high, peduncles 2-5 cm. long; bracts of the involucre 2-seriate, narrowly oblong-lanceolate to lanceolate, acute, hirsute, the outer series greenish, about twice as long as the inner, the inner ones much paler; corolla 2.5 mm. long, the tube glandular, the throat pubescent; rays oblong, 8-10 mm. long, 3-5 mm. broad, pubescent on the outer surface; disk-achenes 2 mm. long, glabrous, epappose, ray-achenes pubescent, bearing a crown of a few bristle-like hairs.

Distribution: calcareous mesas at an elevation of 5000 to 8500 ft., San Luis Potosi and eastern Zacatecas, south to Puebla.

MEXICO: SAN LUIS POTOSI—22° N. lat., alt. 6000-8000 ft., 1887, *Parry & Palmer 445* (F, G, M, US); San Luis Potosi, alt. 5950 ft., Aug. 22, 1926, *Fisher 136* (US); ZACATECAS—near Guadalupe, Aug., 1855, *Schaffner 78* (G); Guadalupe, 1865-66, *Bourgeau 704* (G, US); alt. 8000 ft., Aug. 8, 1898, *Deam 137* (F, G); city of Zacatecas, *Palmer 757* (G); GUANAJUATO—Sept., 1891, *Duges 460* (G); Jaral, 1885, *Schumann 94 (335)* (US); QUERETARO—from "Cierro to San Juan," Aug. 27, 1905, *Altamirano 1744* (US); HIDALGO—Telles, Sept. 21, 1910, *Orcutt 4131* (F, M); Pachuca, Sept. 5, 1910 *Orcutt 3902* (F, M, US); Sierra de Pachuca, alt. 9000 ft., July 21, 1901, *Pringle 9481* (F, G, M, US); calcareous mesas, near Zontecomate, alt. 8500 ft., June 22, 1904, *Pringle 13093* (F, G, US); near Tula, July 3-4, 1905, *Rose, Painter & Rose 8325* (US); PUEBLA—Orizaba Mts., *Botteri 843* (G, US).

4. Zaluzania Robinsonii W. M. Sharp, sp. nov.[13]

Plants suffruticose; stems 3-7 dm. tall, woody below, herbaceous and branched above, sulcate by alternating light green ridges and green grooves, canescent, densely crisp-hirtellous, especially above, sparsely and minutely glandular; leaves petiolate, including the petiole 1.5-6 cm. long, 1-4 cm. broad, of medium texture, crisp-hirtellous and minutely glandular on both surfaces, palmately 3-lobed or tripartite, lobes acute or acutish, subcordate, the anterior lobes divided or sometimes pinnatifid; heads few, in close corymbose clusters, including the rays 8-12 mm. broad, about 5 mm. high, the peduncles of

[13] **Z. Robinsonii** Sharp, sp. nov. Plantae suffruticosae; caulibus 3-7 dm. altis, infra ligneis, supra herbaceis et ramosis, canescentibus, dense crispo-hirtellis; foliis palmater 3-lobatis vel tripartitis, petiolis includentibus 1.5-6 cm. longis, 1-4 cm. latis, lobis acutis, subcordatis, supra et subtus crispo-hirtellis; capitulis radiis includentibus, 8-12 mm. latis, 5 mm. altis; radiis 5-6 mm. longis, tubo dense villoso.—Collected at Cedros, Zacatecas, Mexico, *F. E. Lloyd 124* (M TYPE).

the corymb short, 0.5–3 cm. long; bracts of the involucre 2-seriate, linear-lanceolate, 3 mm. long, acute, ciliate, pubescent; corolla 2.5–3 mm. long, the tube and throat pubescent; rays 5–6 mm. long, tube densely villous; achenes of the disk-flowers glabrous, epappose, ray-achenes cuneate-obovate, densely villous, with a crown of long-villous silky hairs.

Distribution: usually in shade of larger shrubs, hills and mountain slopes of Coahuila south to Zacatecas and Hidalgo.

MEXICO: COAHUILA—valley of Nazar, Bolson de Mapimi, May 11, 1847, *Gregg 631* (M); valley of Nazar, Bolson de Mapimi, collection of 1848–49, *Gregg 447* (G); Parras, 111 miles west of Saltillo, June 18–28, 1880, *Palmer 592* (G, US); Saltillo, June, 1898, *Palmer 360* (F, G, M, U CAL, US); near Saltillo, Nov. 10–20, 1902, *Palmer 279* (F, G, M, US); Parras, 1905, *Purpus 1126* (F, U CAL); Parras, Oct. 6–11, 1898, *Palmer 435* (G, M, U CAL, US); Carneros Pass, Sept. 7, 1889, *Pringle 2402* (F, G, M, U CAL, US); La Ventura, Aug. 2–5, 1896, *Nelson 3930* (G, US); ZACATECAS—Cedros, northern Zacatecas, June, 1908, *Kirkwood 67* (G); in shade of shrubs, vicinity of Cedros, Aug., 1908, *Kirkwood 227* (F); in shade of larger plants, such as mesquite, Cedros, Aug., 1909, *Lloyd 124* (M TYPE); SAN LUIS POTOSI—between the states of Nuevo Leon and Matehuala, June 17–18, 1898, *Nelson 4520* (US); region of San Luis Potosi, Sept. 1879, *Schaffner 717 (286)* (F, US); HIDALGO—mountain slopes, Ixmiquilpan, Sept. 1905, *Purpus 1334* (F, G, M, U CAL).

5. **Zaluzania Grayana** Rob. & Greenm. in Proc. Am. Acad. **34**: 531. 1899; Woot. & Standl. in Contr. U. S. Nat. Herb. [Fl. N. Mex.] **19**: 708. 1915; Blake in Contr. U. S. Nat. Herb. [Standley's Trees & Shrubs Mexico] **23**: 1537. 1926.

Gymnolomia triloba Gray in Proc. Am. Acad. **17**: 217. 1882.

Zaluzania Grayiana Rob. & Greenm. in Proc. Boston Soc. Nat. Hist. **29**: 104. 1899.

Suffruticose; stems from a lignescent rootstock, 4–8 dm. high, branched above, minutely hirtellous to glabrate; leaves petiolate, ovate to 3-lobed, 3–9 cm. long, 1.5–6 cm. broad, the lobes sparsely incised to incised-serrate, acute, minutely hirtellous on both surfaces; heads in loose corymbose clusters, 2–3 cm. broad including the rays, 6–8 mm. high; bracts of the involucre linear-lanceolate, 4 mm. long, minutely hirtellous; pales subcoriaceous, conduplicate, trifid at the apex, ciliate, hirsutulous along the dorsal ridges; ray-flowers 7–10, rays oblong, 0.8–1.5 cm. long, disk-flowers 2 mm. long, the tube hirsutulous, the limb glabrous; achenes of the disk-corollas 2 mm.

long, triangular, epappose, ray-achenes bearing a crown of a few short squamellose setae.

Distribution: mountains of southern Arizona south to Chihuahua.

UNITED STATES: ARIZONA—peaks south of Rucker Valley, 1881, *Lemmon* (G TYPE); near Fort Huachuca, high peaks of Huachuca Mts., Aug.–Sept., 1882, *Lemmon 2764* (F, G, US); Huachuca Mts., July 3, 1884, *Pringle 2145* (G, US); near Ft. Huachuca, Sept., 1894, *Wilcox 469* (US); high peaks of Huachuca Mts., Aug.–Sept., 1882, *Lemmon* (US); north slope of Huachuca Mts., Carr Peak, Aug. 25, *Goodding 864* (G); Apache Pass, Chiricahua Mts., Sept., 1881, *Lemmon* (M).

MEXICO: CHIHUAHUA—shaded ravines, Mapula Mts., alt. 6000 ft., Oct. 30, 1886, *Pringle 755* (F, G, M, US); shaded slopes, La Bufa Mt. above Cusihuiriache, Sept. 2, 1887, *Pringle 1310* (F, G, US).

6. **Zaluzania Pringlei** Greenm. in Proc. Am. Acad. **39**: 101. 1903; Blake in Contr. U. S. Nat. Herb. [Standley's Trees & Shrubs Mexico] **23**: 1538. 1926.

Plants shrubby; stems of the more woody parts covered with a grayish bark, the ultimate branches purplish, striate, lenticular, especially so below, strigose-puberulent above, becoming glabrate below; leaves petiolate, ovate, 3–5.5 cm. long, 1.5–3.5 cm. broad, short-acuminate, acute or submucronate-acute, entire to crenate-dentate, strigose puberulent on both surfaces, petioles slender, 0.5–1.5 cm. long; heads discoid, ovate, grouped in a terminal round-topped paniculate-corymbose cluster, 5–7 mm. high, 5–6 mm. wide; bracts of the involucre 3-seriate, ovate-lanceolate, about 3 mm. long, acute, strigose-puberulent; pales coriaceous, pubescent; achenes 2 mm. long, glabrous, pappus absent.

Distribution: limestone hills of Morelos.

MEXICO: MORELOS—limestone hills near Jojutla, alt. 3000 ft., Oct. 18, 1902, *Pringle 8710* (F, G, M, U CAL, US).

7. **Zaluzania discoidea** Gray in Proc. Am. Acad. **21**: 388. 1886; Rob. & Greenm. in Proc. Am. Acad. **34**: 534. 1899.

Plants herbaceous from a lignescent base; stems 6–10 dm. tall, simple, terminated by a corymbose cluster, striate, purplish, velutinous; leaves short-petiolate, broadly ovate, round-ovate to deltoid-ovate, 4–12 cm. long, 3–10 cm. broad, irregularly crenate to crenate-undulate, obtuse to acute, subcordate

to broadly cordate at the base, palmately veined, pale green above, strigose-velutinous to strigose-hirtellous, whitish beneath, velvety tomentose; heads discoid, in dense corymbose clusters, subglobose, 5–7 mm. broad, 6 mm. high; bracts of the involucre herbaceous, ovate-lanceolate, about 4 mm. long, acute, hirtellous; pales coriaceous, acute, fimbriate; corolla-tube minutely puberulent; achenes about 2.5 mm. long at maturity, glabrous, epappose.

Distribution: rocky hills and mountains of Chihuahua and Durango.

MEXICO: CHIHUAHUA—mountains near Chihuahua, Sept. 12, 1886, *Pringle 1110* (M, U CAL); rocky hills near Chihuahua, Oct. 19, 1885, *Pringle 309* (F, G, US); "Cosiquiriache," Sept. 25, 1846, *Wislizenus 189* (M); DURANGO—El Oro to Guanaceví, Aug. 14–16, 1898, *Nelson 4727* (US); along road between "Cerro Prieto and La Providencia," Sept. 11, 1898, *Nelson 4970* (US).

8. **Zaluzania montagnaefolia** Schz.-Bip. in Flora **44**: 563. 1861; Hemsl. Biol. Cent.-Am. Bot. **2**: 160. 1881; Blake in Contr. U. S. Nat. Herb. [Standley's Trees & Shrubs Mexico] **23**: 1538. 1926.

Ferdinanda montagnaefolia Schz.-Bip. in Koch's Berl. Allgem. Gartenz. 179. 1858.

Zaluzania asperrima Schz.-Bip. in Flora **47**: 218. 1864; Hemsl. Biol. Cent.-Am. Bot. **2**: 159. 1881; Rob. & Greenm. in Proc. Am. Acad. **34**: 532. 1899.

Zaluzania asperrima var. *montagnaefolia* (Schz.-Bip.) Rob. & Greenm. in Proc. Am. Acad. **34**: 532. 1899.

Plants shrubby; stems glabrate below, strigose-hirtellous above; leaves ovate, 2–7 cm. long, 1–3 cm. broad, serrate or crenate-serrate to often entire above, acuminate to acuminate-acute, base decurrent-attenuate, auriculate, leaves of corymbose branches sessile and auriculate, above dark green, pustulate-hispidulous to pustulate-hirsute, beneath light green, densely resinous-glandular and hirsute especially on the veins; heads in corymbose clusters, 1–1.5 cm. broad including the rays; bracts of the involucre 3–4-seriate, ovate, 3–4 mm. long, ciliate, acute to acuminate, hirsutulous; pales subcoriaceous, strongly incurved and united above, the apex resembling the prow of a canoe; ray-flowers styliferous and fertile, 6–8 mm.

long including the achene, base of tube capping the achene; achenes 1.5–2 mm. long, disk-achenes obcompressed-quadrangular, ray-achenes trigonous, glabrous, epappose.

Distribution: dry hills and barrens of Puebla and Oaxaca.

MEXICO: PUEBLA—"dry hills," Tlacuilotepec, Aug., 1909, *Purpus 3824* (F, G, M, U CAL, US); barrens near Tlacuilotepec, May, 1909, *Purpus 3823* (F, G, M, US); Tehuacan, Sept., 1911, *Purpus 5610* (F, M, U CAL); near Tehuacan, Aug. 1, 1901, *Rose & Hay 5954* (US); near Tehuacan, Nov. 7, 1903, *Holway 5347* (G); "in vicinity of San Luis Tultitlanapa near Oaxaca," Aug., 1908, *Purpus 2530* (F, G, M, U CAL, US); OAXACA—"Monte Alban," near Oaxaca, alt. 5800 ft., Oct. 4, 1894, *Pringle 4928* (G, M, U CAL, US); "Monte Alban near Oaxaca City," alt. 5500–5600 ft., Oct. 2, 1894, *Smith 612* (M); "Distrito de Tlacolula, Magdalene Ecatepac," alt. 1700 m., Oct. 23, 1924, *Conzatti 4601* (US); "Cerro de Trujono," *Conzatti 2317* (F).

9. **Zaluzania cinerascens** Schz.-Bip. in Flora **47**: 219. 1864; Blake in Contr. U. S. Nat. Herb. **26**: 249. 1930.

Zaluzania Coulteri Hemsl. Diagn. Sp. Nov. 33. 1879; Biol. Cent.-Am. Bot. **2**: 159. 1881; Rob. & Greenm. in Proc. Am. Acad. **34**: 533. 1899; Blake in Contr. U. S. Nat. Herb. [Standley's Trees & Shrubs Mexico] **23**: 1538. 1926.

Stems suffrutescent at base, apparently simple to the leafy-bracted corymb, conspicuously striate, densely strigulose-hirtellous; leaves broadly ovate to broadly ovate-elliptical, above dark green, strigulose-puberulent, beneath pale green, densely strigose-hirtellous; main cauline leaves 4–13 cm. long, 2–9 cm. broad, becoming smaller above, entire or sparsely serrulate, obtusely acute; heads in corymbose clusters, when mature 1.5–2 cm. broad including the rays, 6–7 mm. high; involucre subhemispherical; bracts oblong-ovate, 4–5 mm. long, acute to obtusish, strigose-pubescent; pales truncate-obtuse, pubescent towards the apex; ray-flowers broadly oblong to oblong, about 1–1.2 cm. long including the achene, 4–6 cm. broad, puberulent on the outer surface; achenes 2 mm. long, glabrous, epappose.

Distribution: fir forests of the Sierra de Pachuca Mts. of Hidalgo at an elevation of 9000 ft. or above.

MEXICO: HIDALGO—Real del Monte, *Coulter 350* (G TYPE); "El Chico," Sept., 1929, *Lyonnet 387* (US); Sierra de Pachuca, alt. 9500 ft., Oct. 6, 1899, *Pringle 7923* (G, US); Sierra de Pachuca, alt. 9500 ft., Aug. 28, 1906, *Pringle 13784* (G, US);

fir forests, Sierra de Pachuca, alt. 9500 ft., Aug. 26, 1902, *Pringle 9997* (F, G, M, US); Sierra de Pachuca, alt. 9000 ft., Aug. 13, 1898, *Pringle 6956* (F, G, M, U CAL, US).

10. **Zaluzania megacephala** Schz.-Bip. in Flora **44**: 563. 1861; *Ibid.* **47**: 218. 1864; Hemsl. Biol. Cent.-Am. Bot. **2**: 159. 1881, in synonymy; Rob. & Greenm. in Proc. Am. Acad. **34**: 533. 1899; Blake in Contr. U. S. Nat. Herb. [Standley's Trees & Shrubs Mexico] **23**: 1538. 1926.

Ferdinanda augusta var. *megacephala* Schz.-Bip. in Flora **44**: 563. 1861.

Plants herbaceous from a perennial rootstalk; stem 6–10 dm. tall, unbranched except in the inflorescence, striate, glabrate below, densely strigose-hirtellous or velutinous above; leaves lanceolate to ovate-lanceolate, 6–10 cm. long, 2–5 cm. broad, serrate, acute, sessile or subsessile, above green, strigose-hirtellous, beneath cinereous, densely strigose-hirtellous to velutinous; heads in corymbose clusters, 1.5–2.5 cm. broad including the rays, 0.8–1.2 cm. high; bracts of the involucre lanceolate, 4–5 mm. long, ciliate, acute to obtuse, puberulent; pales about 5 mm. long, apex acute, slightly incurved; ray-flowers broadly to narrowly oblong, 8–10 mm. long, 3–4 mm. broad; achenes glabrous, 3 mm. long, epappose.

Distribution: mountains of Coahuila.

MEXICO: COAHUILA—mountains near General Zepeda, alt. 6500 ft., Oct. 7, 1905, *Pringle 10076* (F, G, M, U CAL, US); high summits, near Carneros Pass, alt. 10000 ft., Sept. 8, 1889, *Pringle 2398* (F, G, M, U CAL, US); elevated portion of Sierra Madre, 12–14 leagues south of Saltillo, July 25–Aug. 1, 1880, *Palmer 734* (F, G, US).

11. **Zaluzania mollissima** A. Gray in Proc. Am. Acad. **15**: 35. 1880; Hemsl. Biol. Cent.-Am. Bot. **2**: 160. 1881; Rob. & Greenm. in Proc. Am. Acad. **34**: 532. 1899; Blake in Contr. U. S. Nat. Herb. [Standley's Trees & Shrubs Mexico] **23**: 1538. 1926.

Shrubby; stems branched, about 0.5–1.5 m. high, bark grayish-brown, tomentulose above, the more woody parts glabrate; leaves ovate, ovate-lanceolate to oblong-lanceolate, sometimes tending to become trilobed, 2–5 cm. long, 0.5–2.2 cm. broad, entire, obtuse, acute at the base and decurrent on the petiole,

above dark green, tomentulose, beneath cinereous, densely tomentulose; heads three to several in spreading corymbose or paniculate clusters, 2–3 cm. in diameter including the rays, peduncles 1–7 cm. long; bracts of the involucre oblong-ovate, about 4 mm. long, obtuse to acute, velvety tomentose; pales cartilaginous, slightly trilobate; ray-flowers oblong-lanceolate, 1-1.5 cm. long, 3–4 mm. broad, rays bidentate; achenes of the disk glabrous, epappose, ray-achenes slightly pubescent, bearing a crown of short hirsute hairs.

Distribution: in moist soil in fields or among the hills, from Zacatecas to San Luis Potosi.

MEXICO: ZACATECAS—low places, especially where there is relatively abundant moisture, Cedros, May, 1908, *Lloyd 129* (US); hills, Cedros, June, 1908, *Lloyd 32* (G); vicinity of Cedros, 1908, *Kirkwood 129* (F); near Concepcion Del Oro, Aug. 11-14, 1904, *Palmer 314* (F, G, M, U CAL, US); SAN LUIS POTOSI—vicinity of San Luis Potosi, Aug., 1878, *Parry 446* (F, G TYPE, M, US); in fields near "San Miguel," Aug., 1876, *Schaffner 767 (342)* (F, G, US).

12. Zaluzania subcordata W. M. Sharp, sp. nov.[14]

Plants suffruticose; stems branched above, about 0.5–2 m. high, the bark grayish, glabrate below, densely subtomentulose in the inflorescence; leaves broadly ovate to ovate-lanceolate with slender petioles, 1.5–6 cm. long, 0.6–2.5 cm. broad, entire, obtuse, subcordate, above dull green, subtomentose, beneath whitish, densely velvety tomentose, subcoriaceous; heads in close corymbose clusters, 1–1.5 cm. broad including the rays, 6–8 mm. high, peduncles short, 0.5–4 cm. long; bracts of the involucre broadly oblong-lanceolate, 3–4 mm. long, densely tomentulose, whitish; pales trilobed at the summit and fimbriate-ciliate, the outer upper surface pubescent; ray-flowers ovate to oblong-ovate, 5–8 mm. long, 3–4.5 mm. wide, rays faintly bi- or tri-dentate; mature achenes 2–2.5 mm. long,

[14] **Z. subcordata** Sharp, sp. nov. Plantae suffruticosae, caulibus supra ramosis, 0.5–2 m. altis, infra glabratis, dense subtomentosis in inflorescentia; foliis late ovatis vel ovato-lanceolatis, 1.5–6 cm. longis, 0.6–2.5 cm. latis, integris, obtusis, subcordatis, supra obscure viridibus, subtus albidis, dense velutino-tomentosis, subcoriaceis, petiolis gracilibus; capitulis corymbosis, 1–1.5 cm. latis includentibus radiis; radiis ovatis vel oblongo-ovatis, 5–8 mm. longis, 3–4.5 mm. latis.—Collected on rocky hills, Esperanza, Puebla, Mexico, 1907, *Purpus 2580* (F, G, M TYPE, U CAL).

disk-achenes rhomboidally 4-angled, glabrous, epappose, ray-achenes trigonal, pubescent on the ridges, bearing a more or less definite fimbriate-setose or lacerate-setose pappus.

Distribution: rocky or barren hills and mountains of southeastern Puebla.

MEXICO: PUEBLA—rocky hills, Esperanza, Aug., 1907, *Purpus 2580* (F, G, M TYPE, U CAL, US); barren hills about Esperanza, alt. 2660 m., Aug. 17, 1905, *Pittier 452* (US); Esperanza, alt. 2450 m., Nov. 16–19, 1907, *Arsène 7093* (US); Mt. Orizaba, alt. 9000 ft., Aug. 9, 1891, *Seaton 286* (F, G, US); vicinity of San Luis Tultitlanapa near Oaxaca, Aug., 1908, *Purpus 3027* (F, G, M, U CAL, US); Coxcatlan, alt. 8000–9000 ft., Sept., 1909, *Purpus 4121* (U CAL).

13. **Zaluzania augusta** (Lag.) Schz.-Bip. in Flora **44**: 562. 1861; Rob. & Greenm. in Proc. Am. Acad. **34**: 532. 1899; Blake in Contr. U. S. Nat. Herb. [Standley's Trees & Shrubs Mexico] **23**: 1537. 1926.

Ferdinanda augusta Lag. Gen. & Sp. Nov. Pl. 31, *pl. 2.* 1816; DC. Prodr. **5**: 552. 1836.

Anthemis lutescens La Llave & Lexarza, Nov. Veg. Desc. **1**: 26. 1824.

Chrysophania fastigiata Kunth in Less. Syn. Gen. Comp. 224. 1832; DC. Prodr. **5**: 553. 1836.

Ferdinanda lutescens (La Llave & Lexarza) DC. Prodr. **5**: 553. 1836.

Zaluzania angusta Schz.-Bip. in Hemsl. Biol. Cent.-Am. Bot. **2**: 159. 1881.

Plants fruticose; stems 1.5–2.5 m. tall, bark exfoliating, strigose-velvety and glandular on the branches above; leaves ovate to ovate-lanceolate, 2–8 cm. long, 1–3.5 cm. broad, sessile to subsessile above, short-petiolate below, above densely strigose-velutinous, beneath densely cinereous-velvety, lower cauline leaves crenate-serrate, acute at the base, those of the branches entire, acute to acuminately acute; heads numerous, in corymbose clusters, 5–7 mm. broad not including the rays; involucre campanulate, bracts ovate-lanceolate, about 3 mm. long, ciliate, acute, finely strigose; pales subcoriaceous, apex acute and fimbriate-lacerate to somewhat entire; ray-flowers 7–8 mm. long, oblong, bidentate; achenes about 2 mm. long, ray-achenes trigonal, bearing a crown of squamulose setae, disk-achenes rhomboidal in cross-section, glabrous, epappose.

Distribution: rocky mountain slopes and hills, Guanajuato east to Hidalgo and south to Mexico.

MEXICO: GUANAJUATO—"vicinity of Guanajuato," 1895, *Duges 469* (G); QUERETARO—"Cerro de las companas," alt. 1850 m., July 9, 1914, *Arsène 10065* (G, M, US); collected between Cadereyta and Visaron, Aug. 22, 1905, *Rose, Painter & Rose 9738* (G, US); vicinity of Queretaro, alt. 1850 m., 1909–12, *Arsène & Nicolas 6162* (G, M, US); HIDALGO—between Pachuca and Real del Monte, Aug. 31, 1903, *Rose & Painter 6675* (US); near Pachuca, 1899, *Duges* (US); rocky mountain slopes, near Pachuca, Sept., 1905, *Purpus 1539* (F, G, M, U CAL); hills near Tula, alt. 6800 ft., Oct. 14, 1902, *Pringle 9996* (F, G, M, US); MEXICO—hills near Lecheria Station, alt. 7500 ft., Nov. 18, 1903, *Pringle 11614* (G, US); hills near Lecheria, alt. 7600 ft., Aug. 23, 1904, *Pringle 13091* (F, G, US); Rio Hondo Canyon, Aug. 22, 1890, *Pringle 3144* (F, G, M, U CAL, US); near Tlalnepantla, July 6, 1905, *Rose, Painter & Rose 8418* (US); hills near Mexico City, Sept. 5, 1897, *Pringle 7451* (M); "near Guadelupe," Valley of Mexico, Sept. 23, 1903, *Rose, Painter & Rose 7278* (US); "near Guadelupe," Aug. 24, 1865–66, *Bourgeau 803* (G, US).

14. **Zaluzania Sodiroi** Hieron. in Engl. Bot. Jahrb. **29**: 35. 1900.

Zaluzania nonensis Hieron. *l.c.* **29**: 36. 1900.

Zaluzania quitensis Hieron. *l. c.* **29**: 37. 1900.

Plants suffruticose; stems 1–2 m. tall, brownish to purplish pilose-tomentulose, becoming crisp-hirtellous to glabrate; leaves deltoid-ovate, ovate, to ovate-lanceolate, 4–10 cm. long, 2–6 cm. broad, triple-nerved, dentate-mucronate to subentire, acute, base cuneately decurrent on the petiole, above dark green, rugose, scabrate-hirsute, beneath light green, conspicuously reticulate, densely crisp-hirtellous on the veins, globular-resiniferous; heads in corymbose to subcorymbose clusters, 1–1.2 cm. broad including the rays, pedicels 1–2 cm. long; bracts of the involucre triangulate-ovate, obtuse, crisp villous-tomentulose; ray-flowers yellow, oblong, 5–7 mm. long; achenes rhomboidal in cross-section, linear, 2.5–3 mm. long, slightly incurved at the base, glabrous, pappus absent.

Distribution: Ecuador.

SOUTH AMERICA: ECUADOR—arid interandean hills, *Sodiro 31/1* (US ISOTYPE); near Nono, "in silvis subandinis," *Sodiro 31/2* (US); in hills near Quito, *Sodiro 31/3* (US); 4 ft. high, Aug. 28, 1920, near Quito, *Holway 948* (US); Ficoa, near Ambato, Feb., 1919, *Pachano 134* (US); Ambato, *André K1243* (NY); Province of Pichincha, between "La Magdalena and Chillogallo," alt. 2800 m., July 14, 1927, *Firmin 140* (US); Province of Pichincha, between "La Magdalena and Chillogallo," alt. 2810 m., April 19, 1928, *Firmin 471* (US); Province of Chimborazo,

alt. 3000 m., *André K1245* (NY); near Quito, Aug. 1898, *Mille 558* (NY); near Quito, Aug., 1898, *Mille 568* (NY); frequent near "Pifo," alt. 2600 m., 1895, *Mille 569* (US).

BALSAMORHIZA Hooker

History—Hooker[1] in 'Flora Boreali-Americana' in 1834 described two species of *Heliopsis,* namely, *H. ?balsamorhiza* and *H. ?terebinthacea.* However, he doubted their generic position and proposed *Balsamorhiza* as a more appropriate name, due to the abundance of a limpid juice, similar to the resin of *Pinus balsamea,* which exuded from their freshly cut or broken roots. The proposal of this genus is accompanied by a narration of its outstanding characters. DeCandolle[2] and Endlicher[3] treated *Balsamorhiza* as a subgenus under *Heliopsis.*

Nuttall[4] in 1841 gave the first comprehensive study of the genus. Following his generic description he included eight species, namely, *Balsamorhiza Hookeri, B. terebinthacea, B. sagittata, B. helianthoides, B. hirsuta, B. incana, B. macrophylla,* and *B. deltoidea;* the four last being new species. *Balsamorhiza sagittata* and *B. helianthoides* were originally described by Nuttall[5] under *Espeletia.* All the above-named species remain valid except *B. helianthoides* which is synonymous with *B. sagittata.* The genus was divided by Nuttall into two subgenera, namely, Artorhiza and Eubalsamorhiza.

Torrey and Gray[6] and Walpers[7] followed Nuttall's treatment in that they recognized about seven or eight valid species as well as the two subgenera Artorhiza and Eubalsamorhiza.

In 1848 *Balsamorhiza Careyana* was published by Asa Gray[8] in 'Memoirs of the American Academy.' In his 'Synoptical Flora'[9] in 1884 he recognized eight species and one variety. He also introduced the subgenus Kalliactis for those

[1] Hooker, W. J., Fl. Bor.-Am. 1: 310. [1834] 1840.
[2] DeCandolle, A., Prodr. 5: 551. 1836.
[3] Endlicher, S., Gen. Pl. 408. 1838.
[4] Nuttall, T., in Trans. Am. Phil. Soc. II, 7: 349. 1841.
[5] Nuttall, T., in Jour. Acad. Nat. Sci. Phila. 7: 38–39. 1834.
[6] Torrey, J., & Gray. A., Fl. N. Am. 2: 300. 1842.
[7] Walpers, G. G., Rep. Bot. Syst. 2: 610. 1843.
[8] Gray, A., in Mem. Am. Acad. [Pl. Fendl.] N.S. 4: 81. 1848.
[9] Gray, A., Syn. Fl. N. Am. 1[2]: 265. 1884.

species possessing chartaceous rays. This character is not always constant, and therefore his subgenus becomes synonymous with Artorhiza. Between 1890 and 1930 four new species were added to *Balsamorhiza* from the northwestern United States.

GENERAL MORPHOLOGY

Roots.—*Balsamorhiza* develops a fusiform, perennial tap-root with a rough, corrugated, bark-like covering. The inner structure is usually composed of a soft, spongy, woody tissue which secretes a terebinthine, resinous juice when freshly cut or broken. The older roots have a tendency to become more woody. The younger roots of some species, especially in late winter or early spring, have been used as articles of food.

The greatest root development is found in the subgenus Artorhiza. The tap-root is often three feet in length, as in *B. sagittata* and *B. deltoidea.* In these species the crown often develops several underground, horizontal branches. In Eubalsamorhiza the root system is less developed. It consists of a slender tap-root, unbranched above, and usually less than two feet in length. The extensive tap-root system, according to ecological investigations, often extends six feet or more below the surface of the soil, and enables these plants to occupy dry open uplands.

Stem.—It is difficult to say definitely from external examination just where the root ends and the underground stem begins, but according to stelar evidence the crown of the tap-root may be designated as stem. The length of this, however, varies from a few to several inches. The lateral underground branches which are developed especially in *B. sagittata* and *B. deltoidea* originate from a region near the main crown. The development of several such branches from one root gives the plant a close bushy or clumpy habit. In a majority of the species of *Balsamorhiza* the crowns are covered by a dense tuft of persistent, fibrous petiole bases of previous seasons.

The aerial, erect or ascending stems develop each season from the underground crowns. The average height is usually 2–4 dm. The minimum is about 1 dm., as in *B. serrata* and *B.*

hispidula, and the maximum height of 8–10 dm. is often attained in *B. macrophylla.*

The stems are usually subscapose, that is, almost entirely leafless except for a pair of small leaves near the base, as exemplified by a majority of the species of Eubalsamorhiza. The species with leafy or bracteate stems occur in Artorhiza.

Leaves.—The leaves are chiefly opposite, sometimes alternate. Two types of leaf outline are manifest, namely, (1) the ovate to ovate-cordate type, and (2) the oblong-lanceolate pinnate or bipinnatifid type. The name Artorhiza has been assigned to the former group, and Eubalsamorhiza to the latter.

In the section Artorhiza the leaves are either basal or cauline; the cauline alternate types are exemplified in *B. Bolanderi* and *B. invenusta* with ovate or ovate-elliptical outlines. The remaining species, *B. sagittata, B. deltoidea,* and *B. Careyana,* have large, ovate-cordate basal leaves, and bracteate subopposite cauline leaves. The leaf margins in this group are entire, undulate, or dentate with acute apices. The herbaceous texture is common, but in *B. Bolanderi* the leaves become coriaceous and conspicuously reticulated on both surfaces. The subcoriaceous texture is also approached in the more mature leaves of *B. deltoidea* and *B. Careyana,* but the venation never becomes so prominent as in *B. Bolanderi.*

The section Eubalsamorhiza is characterized by a pinnate or bipinnate type of leaf. The pinnate form is the more common; the bipinnate type is characteristic of *B. hirsuta,* and to a less degree of *B. macrolepis.* The subentire leaf is also present in this section. Both pinnate and undivided leaves may occur on the same plant, as in *B. serrata.* In this species the undivided leaves are more common, but in *B. incana* var. *tomentosa* entire or incised leaves are produced. Subentire blades also occur occasionally on the outermost leaves of *B. macrophylla.* The leaves in this section are mostly basal, a pair of small ones being produced on the lower part of the scapose stem.

Pubescence.—The pubescence within the genus is quite diverse—pilose, tomentose, hirsute, velutinous, and sericeous being the common forms. The hairs in a majority of the species

are interspersed by sessile or short-stipitate glands. Frequently the pubescence on the stems is of the pilose nature, interspersed by numerous glands. *Balsamorhiza incana* and its variety *tomentosa* have a covering of long soft tomentum. The usual type of pubescence, however, is the hirsute, hirsute-hispid, or subsericeous.

Inflorescence.—The inflorescence in *Balsamorhiza* consists chiefly of solitary heads which terminate the naked scapose stems. They may be axillary, as in *B. invenusta,* or in raceme-like clusters as in *B. Careyana.* The inflorescence offers no marks of specific importance except in the latter species.

Involucre.—The bracts of the involucre often present important characters for species differentiation, particularly in outline, length with reference to the disk, pubescence, texture, and venation.

The linear-lanceolate to ovate-lanceolate form of involucral bract is the most common. Involucral bracts of this type usually do not exceed the disk in length. An ovate form of bract abruptly constricted above the middle and attenuated to an acute apex is characteristic of *Balsamorhiza hirsuta* and to a less degree of *B. incana.* The bracts of the involucre which exceed the disk in length are foliaceous and mostly oblong or oblong-lanceolate in general outline, as in *B. macrophylla, B. deltoidea,* and *B. macrolepis. Balsamorhiza Bolanderi* is characterized by large, ovate, coriaceous bracts which become glabrate and conspicuously reticulated on both surfaces. The margins of the bracts are entire except in *B. macrolepis* where they are often sparsely serrated or incised.

The pubescence of the involucre is of four sorts, namely, (1) densely tomentose, (2) crisp-pilose, (3) subvelutinous or velvety pubescent, and (4) hirsute or hispid. The densely white-tomentose type of pubescence is exemplified in *B. sagittata* and *B. incana* and its variety *tomentosa. Balsamorhiza serrata* and *B. hirsuta* var. *lagocephala* are the best examples of a dense crisp-pilose-pubescent involucre. A majority of the species, however, are crisp-pilose-ciliate. The velutinous or subsericeous pubescence is characteristic of *B. macrolepis* and

B. Hookeri and its varieties. The hirsute, hispidulus to glabrate condition is also common within the genus.

Receptacle and Pales.—The receptacle in *Balsamorhiza* is broadly convex. The pales are conduplicate and acuminate or acuminate-acute, becoming stiff in the mature heads. They are persistent on the receptacle after the fall of the achenes. Neither the receptacle nor the pales afford any marks that may be used in specific differentiation, but only generic characters.

Corollas.—The heads in *Balsamorhiza* are heterogamous with styliferous and fertile ray-flowers, and usually fertile tubular disk-flowers. *Balsamorhiza invenusta* with eradiate heads, however, is an exception. The corollas in both the ray- and disk-flowers are yellow except in *Balsamorhiza Hookeri* var. *rosea* in which the rays are occasionally purple. The rays are ovate to oblong, subentire, or 2–3-denticulate, styliferous, and accompanied by one or more staminodea. The disk-corollas have a narrow cylindrical tube which expands above into the tubular-campanulate 5-lobed limb.

The stamens are very similar to those described for preceding genera. The style-branches are slender, terete in cross-section, and more or less hirsutulous from base to apex.

Achenes.—The achenes, for the most part, are similar throughout the genus. They are linear-oblong, 5–8 mm. long, and usually glabrous except in *Balsamorhiza Careyana* and *B. Hookeri* var. *rosea* which are pubescent. The disk-achenes are quadrangular, as a rule, with a small rib alternating with each of the four larger angles. *Balsamorhiza invenusta,* however, has rhomboidal disk-achenes and trigonal ray-achenes. The pappus is absent, and only in rare cases in *B. sagittata* has there been observed one or two subulate bristles on each achene.

Geographical Distribution.—The genus *Balsamorhiza* is confined to the northwestern United States. Its center of distribution extends from west-central Wyoming and northern Utah west to southern Washington and northern California. Plants of this genus are mostly inhabitants of dry, usually rocky, open grounds, the deep tap-root system and the low habit enabling them to occupy dry situations.

The subgenus Artorhiza is confined chiefly to the Pacific Coast states, with the exception of *B. sagittata*. This species ranges from the western Dakotas and Colorado west to British Columbia and California, being the most widely distributed species of the genus. *Balsamorhiza deltoidea* is the species with the next widest range, extending from British Columbia southwards to Los Angeles County, California. The remaining species of this section are less widely distributed; for example, *B. Careyana* occurs on dry ground from central and southeastern Washington south to central and northeastern Oregon; while *B. Bolanderi* and *B. invenusta* are confined to central California.

Eubalsamorhiza comprises the greater majority of the species in this genus, but none of the species has a very wide distribution. *Balsamorhiza incana,* having a range from western Wyoming and southwestern Montana west to northeastern Oregon, is the most widely distributed species of the section. *Balsamorhiza macrophylla* and *B. hispidula* occur from western Wyoming and southern Idaho south to Utah and eastern Nevada. The majority of the remaining species are confined to the Pacific Coast region from Washington south to central California.

TAXONOMY

Balsamorhiza [*Balsamorrhiza* of authors] Hook. Fl. Bor.-Am. **1**: 310. [1834] 1840; Nutt. in Trans. Am. Phil. Soc. II. **7**: 349. 1841; Torr. & Gray, Fl. N. Am. **2**: 300. 1842; Walp. Rep. Bot. Syst. **2**: 610. 1843; Benth. & Hook. Gen. Pl. **2**: 366. 1873; Gray, Syn. Fl. N. Am. **1**^{2}: 265. 1884; Hoffm. in Engl. & Prantl. Nat. Pflanzenf. IV. Abt. 5: 234. 1890; Howell, Fl. Northwest Am. **1**: 339. 1900; Coult. & Nels. Bot. Rocky Mts. 545. 1909; Piper & Beattie, Fl. Northwest Coast, 376. 1915; Rydb. Fl. Rocky Mts. 928. 1917; Jepson, Man. Fl. Pl. Cal. 1077. 1925; Blake in Contr. U. S. Nat. Herb. [Tidestrom's Fl. Utah & Nevada] **25**: 582. 1925; Rydb. Fl. Pr. & Pl. Cent. N. Am. 839. 1932.

Roots perennial, fusiform, thick, often becoming very stout in older plants, covered by a rough or corrugated bark. Stems

herbaceous, erect or ascending, leafy, subscapose or scapose, usually unbranched, glabrous or variously pubescent. Leaves opposite or alternate, usually basal, sometimes cauline, ovate-cordate to oblong-lanceolate in general outline, entire, coarsely dentate, incised, pinnately divided to bipinnatifid, acute or acutish, variously pubescent or glabrate. Heads radiate or rarely discoid, usually solitary, sometimes two or more in raceme-like clusters. Bracts of the involucre 2–4-seriate, herbaceous or coriaceous, linear-lanceolate, ovate-lanceolate, ovate-attenuate to oblong, the outer series often foliaceous and longer than the disk, puberulous to densely tomentose. Receptacle broadly convex; pales firm, subcoriaceous, conduplicate, persistent after the fall of the achenes. Disk-flowers light yellow, tube cylindrical, limb tubular to tubular-campanulate, 5-lobed, the base often more strongly developed on one side, glabrous; anther appendages ovate, base sagittate; style-branches slender, attenuate, hirsutulous from base to apex. Rays usually present, fertile, yellow, rarely purplish, oblong-lanceolate, usually 2-denticulate at the apex. Achenes of the disk-flowers fertile, epappose, quadrangulate to subquadrangulate, glabrous or rarely canescent-pubescent, those of the ray-flowers trigonal, otherwise as in the disk-achenes.

Type species: *Balsamorhiza Hookeri* (Hook.) Nutt. in Trans. Am. Phil. Soc. II. **7**: 349. 1841 *(Heliopsis? Balsamorrhiza* Hook. Fl. Bor.-Am. **1**: 310. [1834] 1840).

KEY TO THE SPECIES AND VARIETIES

A. Leaves entire or dentate-serrate, cordate-ovate, deltoid-ovate, ovate or ovate-lanceolate.

B. Stems leafy to inflorescence; leaves alternate, basal and cauline similar in size.

C. Heads discoid; bracts of the involucre lanceolate and usually about as long as the disk .... *1. B. invenusta*

CC. Heads radiate; bracts of the involucre ovate to ovate-lanceolate, foliaceous and much longer than the disk .... *2. B. Bolanderi*

BB. Stems subscapose, bracteate; leaves opposite, basal leaves large, those of the stem reduced.

D. Leaves green on both surfaces, scabrous to hirsute, or hispid; involucre green, glabrate, or hirsute to densely crisp-pilose.

E. Leaves cordate-ovate to deltoid-ovate, entire or coarsely dentate, not conspicuously reticulated.

F. Outer bracts of the involucre lanceolate, seldom exceeding the disk; disk 0.8–2.5 cm. broad; achenes usually cinereous-pubescent..*3. B. Careyana*

FF. Outer bracts of the involucre oblong or oblong-lanceolate, exceeding the disk; disk 2.5–4 cm. broad; achenes glabrous..*4. B. deltoidea*

EE. Leaves lanceolate to ovate-lanceolate, dentate- or serrate-subuliferous, conspicuously reticulated......................*11. B. serrata*

DD. Leaves silvery- to white-tomentose beneath; involucre white, persistently woolly tomentose.

G. Leaves cordate-ovate..........................*5. B. sagittata*

GG. Leaves oblong-ovate to oblong-lanceolate...*9a. B. incana* var. *tomentosa*

AA. Leaves incised, pinnate or bipinnate, lanceolate to oblong-lanceolate in general outline.

H. Leaves canescent or hoary beneath, velutinous, sericeous to tomentose.

I. Leaves velutinous, subsericeous to sericeous.

J. Bracts of the involucre not exceeding the disk, entire.

K. Bracts of the involucre linear-lanceolate, lanceolate to linear-oblong, 2–4 mm. broad, uniformly greenish..................................*6. B. Hookeri*

KK. Bracts of the involucre triangular-acute to ovate-acute, 5–8 mm. broad, usually brownish or hoary at the apex, greenish below................*7. B. platylepis*

JJ. Bracts of the involucre exceeding the disk, often dentate or incised towards the apex..............*8. B. macrolepis*

II. Leaves lanate, floccose-tomentose to tomentose.

L. Leaves lanate; segments narrow, pinnately parted; bracts of the involucre lanceolate.....................................*6b. B. Hookeri* var. *lanata*

LL. Leaves tomentose to floccose-tomentose; segments broadly-lanceolate to ovate-lanceolate, serrate to serrate-incised; bracts of the involucre ovate-attenuate..................................*9. B. incana*

HH. Leaves green on both surfaces, hispid, hirsute to crisp-pilose.

M. Leaves 3–6 dm. long, crisp-hirsute, crisp-pilose to pilose-tomentose.

N. Leaf-segments 5–11 cm. long, entire, crisp-hirsute; bracts of the involucre longer than the disk; petioles glabrous....*10. B. macrophylla*

NN. Leaf-segments 3–6 cm. long, serrate-dentate or incised, crisp-pilose to pilose-tomentose; bracts of the involucre as long as or shorter than the disk; petioles pilose to pilose-tomentose....*10a. B. macrophylla* var. *idahoensis*

MM. Leaves 0.5–4.5 dm. long, hispid, hispid-pilose to hirsute.

O. Achenes pubescent....*6a. B. Hookeri* var. *rosea*
OO. Achenes glabrous.
P. Leaves hispid to hispid-pilose.
Q. Leaves subcoriaceous, segments serrate-subuliferous; bracts of the involucre subuliferous, pilose-tomentose.......
..........................*11. B. serrata*
QQ. Leaves less firm in texture, segments entire, incised or cleft, acute; bracts of the involucre acuminate-acute, hispid-pilose-ciliate.........*12. B. hispidula*
PP. Leaves hirsute to strigose-hirsute.
R. Involucre densely tomentose........
.......*13a. B. hirsuta* var. *lagocephala*
RR. Involucre not tomentose.
S. Bracts of the involucre ovate, abruptly attenuated into long slender, erect apices....*13. B. hirsuta*
SS. Bracts of the involucre linear-lanceolate to ovate-lanceolate, not attenuated, acute.
T. Leaves cleft or parted, the lobes entire.........*14. B. terebinthacea*
TT. Leaves pinnatifid, the segments usually cleft or incised.......
.......*13b. B. hirsuta* var. *neglecta*

1. **Balsamorhiza invenusta** (Greene) Coville in Contr. U. S. Nat. Herb. **4**: 130. 1893; Jepson, Man. Fl. Pl. Cal. 1077. 1925.

Helianthus invenustus Greene, Pittonia, **1**: 284. 1889.

Stems leafy, erect or ascending, 3–6 dm. tall, pilose-hispid, becoming hispidulous below and densely glandular above; leaves petiolate, ovate, ovate-elliptical to ovate-lanceolate, 1–2 dm. long, 4–9 cm. broad, entire to undulate, acute or acuminate, acutish to subcordate at the base, above scabrous to hispid-hirsute, the midrib often pilose-hispid, beneath glandular, hispid to hirsute-pilose on the veins, the petioles hispid-pilose; heads discoid, solitary, terminal or sometimes axillary, 2.5–4 cm. broad; bracts of the involucre about as long as or longer than the disk, oblong-lanceolate, pilose-hirsute-ciliate, glandular on both surfaces, occasionally sparsely hirsute-hispid along the midvein; disk-corolla about 1 cm. long, the throat tubular, glabrous; mature achenes rhomboidal in cross-section, 7–8 mm.

long, the crown developing knob-like projections at the angles, glabrous.

Distribution: forests of south-central California, Fresno, Tulare, and Kern Counties.

CALIFORNIA: Milwood, Fresno Co., July 23, 1892, *Brandegee* (U CAL); Sequoia Nat. Park, Tulare Co., July, 1908, *Davidson 2058* (U CAL); "giant forest," Tulare Co., July, 1905, *Brandegee* (U CAL); North Fork of Middle Fork of Tule River, eastern Tulare Co., July 11, 1908, *Hall 8340* (U CAL); South Fork of Kaweah River, Tulare Co., July 21, 1904, *Culbertson* (F, G, M, NY, U CAL); mountains of Kern Co., 1888, *Palmer 105* TYPE.

This leafy-stemmed species of *Balsamorhiza* is distinguished by its discoid heads, rhomboidal achenes, and tubular corolla. Its general habit resembles that of *Wyethia ovata* Gray.

2. **Balsamorhiza Bolanderi** Gray in Proc. Am. Acad. **7**: 356. 1868; Syn. Fl. N. Am. **1**^{2}: 266. 1884; Jepson, Man. Fl. Pl. Cal. 1078. 1925.

Stems leafy, erect or ascending, unbranched, 1.5–3 dm. high, glandular above in young specimens, becoming glabrous in older plants; leaves mostly cauline, often bearing large scale-like bracts below, ovate, elliptical to broadly ovate-elliptical, 0.5–2.5 dm. long, 4–10 cm. broad, herbaceous in the early stages, becoming glabrous and leathery, conspicuously reticulated on both surfaces, entire, acute or obtuse-apiculate, cordate to acute at the base, young leaves glandular; heads solitary and terminal, 4–6.5 cm. broad including the rays; bracts of the involucre large, foliaceous, ovate to ovate-lanceolate, 2–3 cm. long, herbaceous, becoming coriaceous and conspicuously reticulated in older plants, tomentose-ciliate in the early stages, later glabrous, acute, glandular to glabrate; rays yellow, about 3 cm. long, glabrous; mature achenes quadrangular, 6–7 mm. long, glabrous.

Distribution: along the mountains, Placer Co., southeast to Mariposa Co., California.

CALIFORNIA: Amador Co., June 12, 1889, *Greene* (NY); "Savage Hill," Amador Co., alt. 2200 ft., May, 1891, *Hansen 168* (M, U CAL); sandy hillsides, Auburn, Placer Co., April, 1865, *Bolander 4526* (G TYPE, NY); Bear Valley, Mariposa Co., May 2, 1892, *Congdon* (U CAL); Bear Valley, Mariposa Co., April 12, 1896, *Congdon* (NY, U CAL); Bear Mountain, Mariposa Co., 1865, *Torrey* (NY); "Proner," *Rich* (NY).

This species may be readily distinguished by its conspicuously reticulated, coriaceous leaves, and large involucral bracts, which also become leathery and prominently reticulated.

3. Balsamorhiza Careyana Gray in Mem. Am. Acad. [Pl. Fendl.] N. S. **4**: 81. 1848; Syn. Fl. N. Am. **1**^{2}: 265. 1884; Howell, Fl. Northwest Am. **1**: 339. 1900; Piper in Contr. U. S. Nat. Herb. [Fl. State Wash.] **11**: 580. 1906; Rydb. Fl. Rocky Mts., ed. 2, 929. 1922.

Stems bracteate, one or more arising from the fibrous crowns, 2–6 dm. tall, strigose-hirsute to strigose-hispidulous and glandular above; basal leaves cordate-ovate, cordate-oblong to hastate, 1.5–5 dm. long, 4–13 cm. broad, entire, occasionally coarsely dentate, acute, subcoriaceous, above scabrous, both surfaces green, strigose-hirsute to strigose-hispidulous, and densely to sparsely glandular; cauline leaves opposite, lanceolate to linear-lanceolate, becoming bracteate above; heads radiate, rarely solitary, usually 2 or more in raceme-like or close paniculate clusters, 0.8–2.5 cm. broad excluding the rays; involucre campanulate, the outer series somewhat longer than the inner but rarely longer than the disk, not becoming foliaceous; rays yellow, oblong to oblong-ovate, 2–3 cm. long, bi- or tri-dentate, becoming chartaceous as the head matures; mature achenes linear-oblong, 6 mm. long, ray-achenes 6–7 mm. long, densely canescent-hirsute.

Distribution: dry ground, central and southeastern Washington, south to central and northeastern Oregon.

WASHINGTON: Ellensberg, Kittitas Co., May 20, 1897, *Piper* (NY); Ephrata to Ritzville, Grant Co., June, 1902, *Griffiths & Cotton 483* (NY); Sprague, Lincoln Co., alt. 2000–3000 ft., June, 1893, *Sandberg & Leiberg* (F, G, M, NY, RM, U CAL); dry hillsides, Ritzville, Adams Co., alt. 1451 ft., June 6, 1893, *Sandberg & Leiberg 166* (F, G, M, Ph, NY, U CAL); dry soil, Washtucna, Adams Co., May 18, 1903, *Cotton 976* (G); canyons below Walla Walla, May 23, 1903, *Cotton 1052* (G, M, RM); Walla Walla region, May, 1883, *Brandegee 891* (G, Ph); Prosser, Benton Co., May 27, 1903, *Cotton 1105* (G, M).

OREGON: "Clearwater," *Spalding* (G TYPE, NY, Ph); Pendleton, Umatilla Co., May 15, 1905, *Jones* (NY); near Lexington, Morrow Co., June 5, 1894, *Leiberg 28* (F, G, M, NY, RM); stony, basaltic slope, Bridge Creek, western slope of the Blue Mts., June 22, 1908, *Cusick 3255* (F, G, M, NY, RM, U CAL); hills near Pendleton, Umatilla Co., May–June, 1907, *Cusick 3332* (F, G, M, NY, RM, U CAL); hillsides of "Ochoco River," Crook Co., June 28, 1897, *Cusick 1679* (U CAL); near

"Hoover Creek," Gilliam Co., June 1, 1894, *Leiberg 142* (F, G, M, NY, RM); dry woods, Mt. Hood Forest Reserve, Bear Springs, Wasco Co., July 7, 1929, *Thompson 5171* (Ph).

This species may be distinguished from *B. deltoidea* by the smaller disk and pubescent achenes. The heads are usually in raceme-like clusters, whereas in *B. deltoidea* they are generally solitary. The pubescence of the achene is not always constant. In the region of Wasco and Gilliam Counties, Oregon, where the ranges of the two species overlap, the achenes are invariably glabrous as in *B. deltoidea*, but the other characters are typical *B. Careyana.*

4. **Balsamorhiza deltoidea** Nutt. in Trans. Am. Phil. Soc. II. **7**: 351. 1841; Torr. & Gray, Fl. N. Am. **2**: 302. 1842; Walp. Rep. Syst. **2**: 610. 1843; Gray, Syn. Fl. N. Am. $\mathbf{1^2}$: 266. 1884; Coville in Contr. U. S. Nat. Herb. **4**: 130. 1893; Howell, Fl. Northwest Am. **1**: 339. 1900; Piper in Contr. U. S. Nat. Herb. [Fl. State Wash.] **11**: 580. 1906; Piper & Beattie, Fl. Northwest Coast, 376. 1915; Rydb. Fl. Rocky Mts., ed. 2, 928. 1922; Jepson, Man. Fl. Pl. Cal. 1078. 1925.

Balsamorhiza glabrescens Benth. Pl. Hartw. 317. 1849.

Stems bracteate, 2–8 dm. tall, crisp-pilose to crisp-hirsute, glandular above, glabrate; basal leaves numerous with petioles 1–4 cm. long, the blades cordate-ovate, cordate-oblong to hastate, 0.8–3 dm. long, 0.4–2 dm. broad, entire or occasionally coarsely dentate, becoming subcoriaceous in late stages, acute, both surfaces green, crisp-hirsute to more or less strigose-hirsute, usually glandular, becoming scabrous above; cauline leaves reduced, becoming bracteate above, lanceolate to linear-lanceolate, 3–15 cm. long, 1–3 cm. broad, entire, acute, surface as in the basal leaves, the lowermost pair usually opposite; heads solitary or sometimes two or more, 2.5–4 cm. broad excluding the rays; involucre hemispherical to subhemispherical, bracts oblong-lanceolate to oblong, the outer series foliaceous, longer than the disk, often 3–6 cm. long in later stages, acute or obtuse, the base of the outer bracts often densely crisp-pilose; rays yellow, oblong-lanceolate, 2–4.5 cm. long; mature achenes about 8 mm. long, linear-oblong, glabrous.

Distribution: dry open ground, British Columbia southwards along the Coast Ranges to Los Angeles Co., California.

BRITISH COLUMBIA: Vancouver Island, May 10, 1875, *Macoun 953* (G); Vancouver Island, 1858, *Lyall* (G); vicinity of Victoria, Vancouver Island, May 10, 1893, *Macoun 475* (M, NY); Lake Osoyoos, June 3, 1905, *Macoun 76941* (F); Vancouver Island, May 5, 1908, *Macoun 86299* (F); near "Lost Lake," Victoria, May 23, 1916, *Newcombe 62* (G); "Thetis Lake," Vancouver Island, open wooded hillsides, June 13, 1919, *Carter* (G).

WASHINGTON: Whidbey Island, Clallam Co., *Gardner* (U CAL); Tacoma, Pierce Co., May 20, 1911, *Zeller* (M); Lake View, Pierce Co., May, 1928, *Grant* (RM); Ellensberg, Kittitas Co., June, 1897, *Piper* (RM); Vancouver, Clarke Co., June 8, 1904, *Piper 4945* (G); Klickitat River, near "Mt. Paddo," May 18, 1884, *Suksdorf 364* (G); near Bingen, Klickitat Co., May 5, 1909, *Suksdorf* (NY); Yakima region, 1882, *Brandegee* (M); common on dry grounds, Klickitat Co., April 3, June, 1883, *Suksdorf* (F, Ph); slopes of "Mt. Stuart," July 24, 1893, *Sandberg & Leiberg 573* (G, NY); Painted Rocks, Yakima Co., May 20, 1923, *Nelson 1476* (RM); Tacoma, Pierce Co., May 20, 1911, *Brandell* (M); Rattlesnake Hills, Yakima Co., May 2, 1901, *Cotton 336* (Ph); Lake Chelan, Cascade Mts., Chelan Co., July 1–Sept. 15, 1915, *Kammerer 60* (M); dry prairies near Ft. Lewis, Pierce Co., April 26, 1930, *Thompson 5133* (M).

OREGON: "near the outlet of the Wahlamet," May, 1835, *Nuttall* (G, NY, Ph TYPE); near Philmath, Benton Co., May 31, 1919, *Holmes* (M); Forest Grove, Washington Co., May, 1884, *Drake & Dickson* (F); hillsides near Dalles, Wasco Co., April 19, 1903, *Lunell 67* (G); hillsides and prairies, Hood River Co., April 26, 1924, *Henderson 362* (M); hillsides, Deer Creek, near Selma, Josephine Co., April 11, 1926, *Henderson 5702* (M, RM); west shore of Summer Lake, Lake Co., June 3, 1911, *Eggleston 6820* (NY); high ground, Monmouth, Polk Co., May 20, 1893, *Page 216* (F); hillsides, Scoggin's Village, Washington Co., May 20, 1896, *Lloyd* (NY); dry ridge, 4 mi. west of Table Rock, Clackamas Co., May 30, 1924, *Peck* (WU); dry slope, Ashland, Jackson Co., July 14, 1913, *Peck* (WU); dry hillsides, the Dalles, Wasco Co., April 7, 1914, *Peck 5040* (WU); Wimer, Jackson Co., June 29, 1892, *Hammond 209* (M, NY, Ph, RM); Salem, Marion Co., 1871, *Hall 276* (F, G, M); dry ground near Hood River, Hood River Co., April 3, 1926, *Thompson 661* (M); "Scraggins" Valley, Washington Co., May 21, 1927, *Thompson 2495* (Ph); open pastures near Estacada, Clackamas Co., June 11, 1927, *Thompson 2593* (Ph); hills near Brownsboro, Jackson Co., April 10, 1927, *Thompson 2163* (Ph); open sandy hillsides, Hood River, Hood River Co., May 10, 1920, *Gorman* (Ph); hill, one mile east of Mosier, Wasco Co., May 5, 1928, *Gale 111* (M, Ph); open ground, Salem, Marion Co., May 2, 1917, *Nelson 1091* (G); border of field, 3 miles south of Salem, Marion Co., April 23, 1921, *Nelson 3506* (Ph); dry open woods, Grants Pass, Josephine Co., April 20, 1912, *Prescott 11* (G); Dalles, Wasco Co., April, 1882, *Howell* (NY); June, 1881, *Howell* (F, G, Ph).

CALIFORNIA: Kernville, Kern Co., May 14, 1892, *Brandegee* (U CAL); between Auburn and Coal, Eldorado Co., April 28, 1909, *Brandegee* (U CAL); Water Canyon, Tehachapi Mts., Kern Co., alt. 6000 ft., June 26, 1908, *Abrams & McGregor 833* (NY); Liebre Mts., Los Angeles Co., alt. 4500 ft., June 20–23, 1908, *Abrams & McGregor 356* (G, NY); Cantara, Siskiyou Co., May 23, 1923, *Eastwood 11927* (M); Tehachapi, Kern Co., May 13, 1913, *Eastwood 3237* (G, NY); near Inde-

pendence, Inyo Co., alt. 5500 ft., *Hall & Chandler 7304* (M, U CAL); south slope near Kernville, Kern Co., alt. 5000 ft., June 1904, *Hall & Babcock 5100* (U CAL); Tejon Pass, Los Angeles Co., June, 1905, *Hall 6263* (U CAL); in grassy spots among pines, Sierra Nevada foothills, Eldorado Co., April 13, 1921, *Hall 11246* (U CAL); hillsides beneath pines, Yosemite Nat. Park, Mariposa Co., June 10, 1911, *Hall 8907* (U CAL); on Moro Creek, San Rafael Mts., Santa Barbara Co., May 18, 1907, *Hall 7797* (Ph, RM, U CAL); Blue Cañon, Placer Co., alt. 4701 ft., June 24, 1908, *Walker 1285* (U CAL); Mendocino Co., 1866, *Bolander 6187* (F, G, M, NY); dry open stony slopes, Back Mt., Humboldt Co., *Tracy 4175* (U CAL); Burnt Ranch, Trinity Co., alt. 1500 ft., April 27, 1924, *Tracy 6662* (U CAL); open woods, Trinity River Valley, Humboldt Co., alt. 600 ft., May 17, 1925, *Tracy 6984* (U CAL); Tehachapi Valley, Kern Co., May 11, 1896, *Davy 2185* (U CAL); open ground, "Rawhide Hill," Tuolumne Co., May 30, 1919, *Williamson 185* (NY); Keene Station, Kern Co., May 1, 1905, *Heller 7802* (G, M, NY, Ph); on the Newville-Cuelo Road, Glenn Co., alt. 3000 ft., June 16, 1915, *Heller 11977* (M); dry soil, Siskiyou Co., April 14, 1909, *Butler 595* (U CAL); Klamath Hills, Siskiyou Co., April 16, 1910, *Butler 1180* (M, RM, U CAL); near Yreka, Siskiyou Co., April 25, 1876, *Greene 718* (F, G, M, NY); region of Tehachapi Peak, Kern Co., June 25, 1895, *Dudley 363* (F, NY, U CAL); Sonoma Co., coll. of 1853–54, *Bigelow* (G, NY); open hills near "French Flat," Tuolumne Co., alt. 1450 ft., April 11–16, 1919, *Ferris 1580* (NY); "Mt. Sanhedrin," Mendocino Co., June 7, 1893, *Blankinship* (G).

The leaves of *B. deltoidea* are of relatively thin texture in the early stages, but after the flowering season they become more or less coriaceous. This occurrence is more common in the southern part of its range.

5. **Balsamorhiza sagittata** (Pursh) Nutt. in Trans. Am. Phil. Soc. II. **7**: 350. 1841; Torr. & Gray, Fl. N. Am. **2**: 301. 1842; Walp. Rep. Bot. Syst. **2**: 610. 1843; Gray in Mem. Am. Acad. [Pl. Fendl.] N. S. **4**: 82. 1848; Syn. Fl. N. Am. **1**^{2}: 265. 1884; Howell, Fl. Northwest Am. **1**: 339. 1900; Piper in Contr. U. S. Nat. Herb. [Fl. State Wash.] **11**: 580. 1906; Coult. & Nels. Bot. Rocky Mts. 545. 1909; Rydb. Fl. Rocky Mts., ed. 2, 928. 1922; Blake in Contr. U. S. Nat. Herb. [Tidestrom's Fl. Utah & Nevada] **25**: 582. 1925; Jepson, Man. Fl. Pl. Cal. 1078. 1925; Rydb. Fl. Pr. & Pl. Cent. N. Am. 839. 1932.

Buphthalmum sagittatum Pursh, Fl. Am. Sept. **2**: 564. 1814.

Balsamorhiza helianthoides Nutt. in Trans. Am. Phil. Soc. II. **7**: 351. 1841; Torr. & Gray, Fl. N. Am. **2**: 302. 1842; Walp. Rep. Bot. Syst. **2**: 610. 1843.

Espeletia helianthoides Nutt. in Jour. Acad. Nat. Sci. Phila. **7**: 39. 1834.

Espeletia sagittata Nutt. *Ibid.* 38. *pl. 4.* 1834.

Stems leafless or bracteate, one to several from a single crown, 2–6.5 dm. tall, tomentose below, densely tomentose above; leaves basal, cordate-ovate, cordate-oblong to hastate, 2–4 dm. long, 0.5–1.5 dm. broad, entire, acute, above cinereous-strigulose, beneath silvery tomentulose to velutinous; heads usually solitary, sometimes 2–3, 6–11 cm. broad including the rays; bracts of the involucre ovate-lanceolate to lanceolate, the outer series longer than the inner, acuminate to attenuate, densely white-tomentose; pales long-attenuate, terminating in an awl-like apex, pilose-ciliate; rays yellow, oblong-lanceolate, 2–4 cm. long, 0.8–1.5 cm. broad, tube crisp-pilose; mature achenes linear-oblong, 7–8 mm. long, glabrous.

Distribution: dry ground, South Dakota and Colorado, west to British Columbia and California.

SOUTH DAKOTA: limestone, Black Hills Nat. Forest, June 15, 1910, *Murdock 4096* (F, G); limestone, west of Custer, Custer Co., alt. 6000–6500 ft., July 29, 1892, *Rydberg 808* (G, NY).

MONTANA: hills near Midvale, Teton Co., June 16, 1903, *Umbach 60* (F); near Great Falls, Cascade Co., May 2, 1886, *Anderson* (U CAL, M); near Butte, Silverbow Co., 1893, *Moore* (M); Bridger Mts., Gallatin Co., June 11, 1897, *Rydberg & Bessey 5174* (F, G, NY, RM); Custer, Yellowstone Co., May 30, 1890, *Blankinship 52* (G, M); near Missoula, Missoula Co., May 19, 1924, *Kirkwood 1732* (RM, U CAL); Helena, Lewis and Clark Co., June 24, 1888, *Kelsey* (U CAL); Flathead region, Flathead Co., 1883, *Ayres 63* (Ph); Flathead River, 1834, *Nuttall* (Ph TYPE).

WYOMING: Laramie Hills, Albany Co., June, 1908, *Nelson 9140* (RM); Evanston, Uinta Co., June 4, 1898, *Nelson 4518* (RM); hills, Bush Ranch, Sweetwater Co., June 10, 1900, *Nelson 7084* (RM); dry soil, Leucite Hills, Sweetwater Co., June 18, 1901, *Merrill & Wilcox 686* (G, RM); Glen Creek, Yellowstone National Park, July 1, 1899, *Nelson & Nelson 5613* (G, M, NY, RM); Little Goose Canyon, Sheridan Co., June 22, 1913, *Sharp 356* (RM); Fremont Lake, Fremont Co., June 29, 1904, *Warren* (RM); near Rawlins, Carbon Co., June 30, 1899, *Pammel 75* (M); dry rocky flats, Grand Teton National Park, June 17, 1933, *Williams 1125* (M); dry open ground, near the "Devil's Tower," Crook Co., June 27, 1929, *Palmer* (G).

COLORADO: Cimarron, Montrose Co., alt. 7000 ft., May 19, 1898, *Crandall 2723* (F, G, NY, Ph, RM); Rio La Plata, La Plata Co., June, 1875, *Brandegee 1077* (U CAL); Mesa Verde National Park, May 27, 1925, *Schmoll & Nusbaum 1574* (RM); Cerro Summit, Montrose Co., alt. 8000 ft., June 7, 1901, *Baker 51* (G, M, NY, RM, U CAL); Norwood Hill, San Miguel Co., Aug. 16, 1912, *Walker 466* (G, M, RM); open meadows, near Naturita, Montrose Co., alt. 7000 ft., May 25, 1914, *Payson 343* (F, G, M, RM).

UTAH: Ogden, Weber Co., July 1, 1880, *Engelmann* (M); hillsides, Wheelon-

Collinston, Boxelder Co., May 1, 1911, *Smith 2348* (NY); Fort Douglas, Salt Lake Co., May 5, 1908, *Clemens* (F, G, Ph); dry hillsides, Daggett Co., May 28, 1932, *Williams 415* (NY, RM).

IDAHO: Kootenai Co., July, 1890, *Leiberg* (F, NY); Boise, Ada Co., alt. 2880 ft., May 27, 1911, *Clark 28* (F, G, M, RM, U CAL); Montpelier, Bear Lake Co., May 20, 1910, *Macbride 202* (G, M, RM); near Lewiston, Nez Perces Co., April 27, 1896, *Heller & Heller 2958* (F, M, NY, Ph); New Plymouth, Canyon Co., alt. 2200 ft., May 21, 1910, *Macbride 79* (G, M, NY, RM).

NEVADA: Pyramid Lake, Washoe Co., June 1, 1913, *Kennedy 1985* (M, Ph, U CAL); King's Cañon, Ormsby Co., June 1, 1902, *Baker 926* (G, M, NY, RM, U CAL); Carson City, 1863, *Anderson 173* (G).

BRITISH COLUMBIA: between Midway and Lake Osoyoos, May 5, 1905, *Macoun 76942* (NY); Spencer's Bridge, May 26, 1889, *Macoun* (G).

WASHINGTON: Pullman, Whitman Co., June 1, 1893, *Piper 1594* (F, G, NY); Hangman Creek, Spokane Co., alt. 1510 ft., May 17, 1893, *Sandberg & Leiberg 23* (F, G, M, NY, Ph, RM, U CAL); rocky slopes, north of Entiat, Chelan Co., April 18, 1931, *Thompson 5985* (G, NY); open slopes, Beverly Creek, Kittitas Co., May 16, 1931, *Thompson 6386* (G); hillsides near Waitsburg, Walla Walla Co., April 21, 1897, *Horner B277* (G); among sage-brush near Coulee City, Grant Co., May 2, 1931, *Thompson 6126* (G).

OREGON: near North Powder, Union Co., May 10, 1928, *Gale 255* (Ph); Wallowa Co., April 30, 1927, *Gabrielson* (Ph); near Lone Rock, Lillian Co., alt. 890 m., May 25, 1894, *Leiberg 114* (F, NY, U CAL); 15 mi. n. e. of Pendleton, Umatilla Co., May 17, 1923, *Sherwood 372* (F, WU); dry ground, Harney Co., June 28, 1912, *Peck 3071* (WU); sagebrush, Brogan, Malheur Co., 1910, *Cooper 1182* (WU); Dog Mt., Lake Co., July 8, 1927, *Peck 15544* (M).

CALIFORNIA: Alpine Co., June, 1892, *Hansen 420* (M); American Valley, Plumas Co., June, 1875, *Austin 94* (U CAL); on Sierra Nevada, above Jonesville, Butte Co., alt. 7000 ft., June 16, 1915, *Heller 12026* (F, G, M); open places in the yellow-pine forest at Mineral, Tehama Co., May 30, 1928, *Heller 14594* (M, NY); Goose Lake Valley, Modoc Co., May, 1894, *Austin 47* (U CAL); Deer Park, Placer Co., alt. 6500 ft., *Walker 2016* (M, RM).

6. **Balsamorhiza Hookeri** Nutt. in Trans. Am. Phil. Soc. II, **7**: 349. 1841; Torr. & Gray, Fl. N. Am. **2**: 301. 1842; Walp. Rep. Bot. Syst. **2**: 610. 1843; Gray, Syn. Fl. N. Am. **1**^{2}: 266. 1884; Howell, Fl. Northwest Am. **1**: 340. 1900; Coult. & Nels. Bot. Rocky Mts. 546. 1909; Blake in Contr. U. S. Nat. Herb. [Tidestrom's Fl. Utah & Nevada] **25**: 583. 1925, in part; Jepson, Man. Fl. Pl. Cal. 1078. 1925, in part.

Heliopsis (?) *Balsamorrhiza* Hook. Fl. Bor.-Am. **1**: 310. [1834] 1840; DC. Prodr. **5**: 551. 1836.

Balsamorrhiza Balsamorrhiza (Hook.) Heller in Cat. N. Am. Pl. 7. 1898; Piper in Contr. U. S. Nat. Herb. [Fl. State Wash.] **11**: 581. 1906; Piper & Beattie, Fl. Northwest Coast, 376. 1915.

Stems scapose, 1–3 dm. tall, pilose near the heads, otherwise subsericeous; leaves ovate-lanceolate to lanceolate, pinnately incised or divided, 1–3 dm. long, the divisions cleft into several spreading or ascending, acute or entire lobes, 1–4 cm. long, 0.5–1 cm. broad, subvelutinous-canescent on both surfaces, often densely so on the younger leaves, of medium texture; heads solitary, 4–7 cm. broad including the rays; bracts of the involucre linear-lanceolate to linear-oblong, about as long as or shorter than the disk, acute, pilose; rays yellow, oblong to ovate-oblong, 1.5–2.5 cm. long, bifid or entire, tube and lamina pubescent; achenes 4–5 mm. long, glabrous.

Distribution: moist grounds, Yakima and Klickitat Counties, west to Clark County, Washington.

WASHINGTON: near the mouth of the Columbia River, "1834–35," *Nuttall* (G, Ph, NY); Tampico, Yakima Co., April 6, 1924, *Nelson 1595* (RM); Simcoe Mts., Yakima Co., June, 1881, *Howell* (NY); prairies, Simcoe Mts., Yakima Co., *Howell* (G); low grounds, Falcon Valley, Klickitat Co., May 20, 1881, *Suksdorf* (F, Ph); low grounds in open woods, Falcon Valley, Klickitat Co., May 3, 1884, *Suksdorf 357* (G); Klickitat River, Klickitat Co., May 18, 1884, *Suksdorf 359* (G); Falcon Valley, Klickitat Co., May 3, 1884, *Suksdorf 363* (G); Mill Plain, Clark Co., June 4, 1880, *Howell* (F).

6a. var. **rosea** (Nels. & Macbr.) W. M. Sharp, comb. nov.

Balsamorhiza rosea Nels. & Macbr. in Bot. Gaz. **56**: 478. 1913.

Stems about 1 dm. tall, purplish; leaves .8–1.2 dm. long, strigose-hirsutulous; rays yellow or purplish; achenes 5–6 mm. long, pubescent; in all other characters similar to the species.

Distribution: thin rocky ridges of Rattlesnake Mts., Yakima Co., Washington.

WASHINGTON: ridges of Rattlesnake Mts., Yakima Co., May 8, 1902, *Cotton 568* (G, M, Ph, RM TYPE).

6b. var. **lanata** W. M. Sharp, var. nov.[10]

Leaves 1–2.5 dm. long, bipinnately divided, the segments narrow, 1.5–5 cm. long, 0.5–1 cm. broad, lanceolate, acute, lanate

[10] B. Hookeri var. lanata W. M. Sharp, var. nov., foliis 1–2.5 dm. longis, pinnatisectis, segmentis angustis, 1.5–5 cm. longis, 0.5–1 cm. latis, lanceolatis, acutis, utrinque lanatis; petiolis dense lanatis; bracteis involucri lanceolatis, acuminatis, lanatis. Cetera speciei similis.—Collected near Yreka, Siskiyou Co., California, May 2, 1876, *Greene 745* (F, G, M TYPE).

on both surfaces; petioles densely lanate; bracts of the involucre lanceolate, acuminate, lanate; other characters similar to the species.

Distribution: dry hills near Yreka, Siskiyou Co., California.

CALIFORNIA: near Yreka, Siskiyou Co., May 2, 1876, *Greene 745* (F, G, M TYPE); dry hills near Yreka, Siskiyou Co., April 9, 1910, *Butler 1157* (M, RM, U CAL); near Yreka, Siskiyou Co., April, 1903, *Mooney* (U CAL).

7. **Balsamorhiza platylepis** W. M. Sharp, sp. nov.[11]

Stems scapose, 1–3.5 dm. high, with cinereous-appressed pubescence; leaves pinnately divided, 1–3 dm. long, the divisions 2–5 cm. long, 0.5–1.5 cm. broad, entire, coarsely serrate to incised, acute, above light green, velutinous to subsericeous, beneath silvery sericeous to velutinous; heads solitary, 4–6 cm. broad including the rays; bracts of the involucre equalling or shorter than the disk, triangular to ovate, acute, 1–2 cm. long, 5–8 mm. broad, outer series brownish or hoary at the apex, greenish below, sericeous to velutinous; rays yellow, broadly oblong, 2–3.5 cm. long, .5–1 cm. broad, bifid or entire, tube and lamina pubescent; achenes 6–8 mm. long, glabrous, epappose.

Distribution: dry gravelly or rocky ground, southern Oregon, southward to west-central Nevada and northern California.

NEVADA: Marmol Station, Washoe Co., alt. 5000 ft., May 30, 1912, *Kennedy 1859* (F TYPE, G, M, NY); near Verdi, Washoe Co., May 5, 1895, *Sonne* (NY).

OREGON: serpentine ridge northwest of Selma, Josephine Co., April 13, 1924, *Thompson 2272* (WU); hillsides near Waldo, Josephine Co., April, 1887, *Howell* (M, NY); serpentine hills along Deer Creek, north of Selma, Josephine Co., March 29, 1926, *Henderson 5703* (RM); "Quartz Valley," 1893, *Austin* (U CAL).

CALIFORNIA: Modoc Co., July, 1898, *Austin & Bruce 2179* (NY, U CAL); Goose Lake Valley, Modoc Co., May, 1894, *Austin* (U CAL, Ph); lava beds near Egg Lake, Modoc Co., June 8, 1894, *Baker & Nutting* (RM, U CAL); Goose Valley, Shasta Co., June–July, 1912, *Eastwood 896* (G, NY); Plumas Co., 1879, *Austin*

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[11] **B. platylepis** W. M. Sharp, sp. nov., caulibus scaposis, 1–3.5 dm. altis, adpresso-cinereo-pubescentibus; foliis pinnatisectis, 1–3 dm. longis, segmentis 2–5 cm. longis, 0.5–1.5 cm. latis, integris, grosse serratis vel incisis, acutis, supra pallide viridibus, plus minusve velutinis vel subsericeis, subtus argenteo-sericeis vel velutinis; bracteis involucri disco aequalibus vel brevioribus, triangulatis vel ovatis, acutis, 1–2 cm. longis, 5–8 mm. latis, exterioribus ad apicem fulvis aut albidis, subtus viridibus, sericeis vel velutinis.—Collected at Marmol Station, Washoe Co., Nevada, alt. 5000 ft., *Kennedy 1859* (F TYPE, G, M, NY).

(G); near Truckee, Nevada Co., June 7, 1917, *Hall 10327* (U CAL); Dog Valley, Sierra Co., May, 1892, *Sonne 368* (M); Hobart Mills, Nevada Co., May–June, 1925, *Drew* (RM).

8. **Balsamorhiza macrolepis** W. M. Sharp, sp. nov.[12]

Stems usually scapose, 2–6 dm. high, below appressed-pilose, above appressed or spreading pubescent; leaves pinnately divided to bipinnatifid, 2.5–5 dm. long, the divisions lanceolate in general outline, 3–10 cm. long, 0.5–2 cm. broad, entire, incisely toothed or again pinnatifid, acute, above green, subvelutinous, beneath light green to canescent, densely subsericeous to velutinous, glandular; heads solitary, radiate, 4–8 cm. broad including the rays; bracts of the involucre 3-seriate, the outer series large, twice as long as the disk, oblong to oblong-lanceolate, 2–3.5 cm. long, 0.5–1.3 cm. broad, obtuse or abruptly acuminate, often dentate or incised towards the apex, minutely velutinous; rays yellow, oblong-elliptical, 2.5–3 cm. long, 1–1.5 cm. broad, tube and lamina puberulent to glabrous; achenes linear-oblong, 5–7 mm. long, quadrangular, glabrous.

Distribution: north-central California, Butte Co., southeast to Mariposa Co., southwest to Sonoma and Santa Clara Counties.

CALIFORNIA: Clear Creek, Butte Co., May 1–15, 1897, *Brown 208* (F, M, NY TYPE, Ph, RM); Brush Creek, Butte Co., 1908, *Konger 122843* (U CAL); fields, Butte Co., May 1898, *Bruce 2469* (NY); sandy hillsides near Lincoln, Placer Co., April 15, 1917, *Ramaley 11109* (U CAL); Amador, Amador Co., alt. 1000 ft., May, 1895, *Hansen 1069* (M); Sonoma, Sonoma Co., 1853–54, *Bigelow* (G, NY); Cedar Mt., Alameda Co., May, 1903, *Elmer 4374* (M, NY, U CAL); Oakland Hills, near Oakland, Alameda Co., June 6, 1868, *Kellogg & Harford 430* (NY, G); San Martin, Santa Clara Co., March 30, 1901, *Chandler 914* (U CAL); Bear Mt., Mariposa Co., 1865, *Torrey* (M); "Coulterville Road," Yosemite Nat. Park, Mariposa Co., alt. 4500 ft., June 7, 1911, *Hall 8885* (U CAL); "Kirby Ranch," Mariposa Co., May, 1886, *Congdon* (U CAL).

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[12] **B. macrolepis** W. M. Sharp, sp. nov., caulibus 2–6 dm. altis, infra adpresse pilosis, supra adpresse vel laxe pubescentibus; foliis pinnatiscissis vel bipinnatifidis, 2.5–5 dm. longis, segmentis lanceolatis, 3–10 cm. longis, 0.5–2 cm. latis, integris, incisis aut pinnatifidis, acutis, supra viridibus et subvelutinis, subtus pallide viridibus vel canescentibus et plus minusve dense subsericeis vel velutinis, glandulosis; bracteis involucri 3-seriatis, exterioribus magnis, disco duplo longioribus, oblongis vel oblongo-lanceolatis, 2–3.5 cm. longis 0.5–1.3 cm. latis, obtusis aut acuminatis, saepe ad apicem dentatis vel incisis, minute velutinis.—Collected at Clear Creek, Butte Co., California, May 1–15, 1897, *Brown 208* (F, M, NY TYPE, Ph, RM).

This species may be readily distinguished from other species of *Balsamorhiza* by its large puberulous, oblong bracts 2–3 cm. long, large leaves 2.5–5 dm. long, and its soft subvelutinous pubescence. This is the only pinnate-leaved species of this genus occurring in California south of Butte County.

9. **Balsamorhiza incana** Nutt. in Trans. Am. Phil. Soc. II. **7**: 350. 1841; Torr. & Gray, Fl. N. Am. **2**: 301. 1842; Walp. Rep. Bot. Syst. **2**: 610. 1843; Howell, Fl. Northwest Am. **1**: 340. 1900; Coult. & Nels. Bot. Rocky Mts. 546. 1909; Rydb. Fl. Rocky Mts., ed. 2, 929. 1922; Blake in Contr. U. S. Nat. Herb. [Tidestrom's Fl. Utah & Nevada] **25**: 582. 1925.

Balsamorrhiza Hookeri var. *incana* (Nutt.) Gray, Syn. Fl. N. Am. 1^2: 266. 1884.

Balsamorrhiza floccosa Rydb. in Bull. Torr. Bot. Club **27**: 629. 1900; and Fl. Rocky Mts., ed. 2, 929. 1922.

Stems subscapose, 1.5–4 dm. tall, white-tomentose to lanate-tomentose; leaves lanceolate to oblong-lanceolate, pinnately divided, 1–4 dm. long, the divisions lanceolate, oblong-lanceolate to ovate-lanceolate, 1.5–6 cm. long, 0.5–2.5 cm. broad, entire, coarsely serrate or serrate-incised, acute, above light green, beneath cinereous, both surfaces tomentose to floccose-tomentose, petioles tomentose to lanate-tomentose; heads solitary, 7–11 cm. broad including the rays; bracts of the involucre 3-seriate, ovate-attenuate to lance-attenuate, about as long as the disk, densely white-tomentose to floccose-tomentose; pales attenuate-subulate, pilose on the upper half; rays yellow, oblong, 3–4.5 cm. long, 0.5–1 cm. broad, bifid or entire, tube and base of lamina pilose-tomentose; disk-flowers 9–10 mm. long, glabrous; achenes linear-oblong, 5–6 mm. long, glabrous.

Distribution: southwestern Montana and western Wyoming to Washington and Oregon.

MONTANA: Spanish Basin, Gallatin Co., a[illegible]000 ft., July 1, 1897, *Rydberg & Bessey 5175* (F, G, NY, RM); "Camp Creek, [illegible]une 12, 1905, *Jones* (U CAL).

WYOMING: Rocky Mountains, 1834, *Nuttall* (Ph TYPE); Three Forks of the Missouri and Yellowstone Rivers, June 30, 1860, *Hayden* (M); dry soil, "Big Sandy River near Leckie," June 22, 1901, *Merrill & Wilcox 743* (G, RM, NY); eastern slope of the Big Horn Mts., headwaters of Clear Creek, Johnson Co., alt. 7000–9000 ft., July 20–Aug. 15, 1900, *Tweedy 3150* (RM, NY); Rattlesnake Mts.,

Natrona Co., July 29, 1898, *Nelson 4993* (M, RM, NY); near Big Horn, Sheridan Co., alt. 5000 ft., July 2, 1897, *Pammel & Stanton 322* (M); Little Goose Cr., Sheridan Co., July 16, 1896, *Nelson 2342* (RM, M); headwaters of the Tongue River, Big Horn Mts., Sheridan Co., July, 1898, *Tweedy 11* (NY); Wind River Range, June, 1873, *Parry 165* (M, Ph, NY); Little Bald Mt., Big Horn Mts., Bighorn Co., alt. 9500 ft., July 13, 1900, *Jack* (G); Wind River Valley, May 18, 1860, *Hayden* (M); Big Horn Mts., Sheridan Co., alt. 7500 ft., July, 1899, *Tweedy 2115* (NY).

IDAHO: about Lake Waha, Nez Perces Co., alt. 3500–4000 ft., June 22, 1896, *Heller & Heller 3298* (M, Ph, NY, U CAL); Clearwater, *Spalding* (G, Ph); Craig Mts. at Lake Waha, Nez Perces Co., May 24, 1892, *Sandberg, MacDougal & Heller 248* in part (F, G, NY).

WASHINGTON: open slopes near Lindel, Asotin Co., May 20, 1928, *St. John & Brown 3900* (Ph); Blue Mts., Columbia Co., June 11, 1887, *Horner* (G).

OREGON: Cabbage Hill east of Pendleton, Umatilla Co., May 10, 1928, *Gale 178* (M); dry open ground near Pendleton, Umatilla Co., June 24, 1927, *Gabrielson* (Ph, WU); 3 miles south of Elgin, Union Co., May 22, 1923, *Sherwood 323* (WU, F); "Camas prairie," July, 1902, *Griffiths & Hunter 77* (NY).

9a. var. **tomentosa** (Rydb.) W. M. Sharp, comb. nov.

Balsamorrhiza tomentosa Rydb. in Bull. Torr. Bot. Club. **27**: 628. 1900; Fl. Rocky Mts., ed. 2, 928. 1922.

Leaves oblong-ovate to oblong-lanceolate, 2.5–4 dm. long, 3–8 cm. broad, subentire, dentate-lacerate to incised, acute, above light green, tomentose to lanate-tomentose, beneath whitish, densely tomentose; bracts of the involucre linear-lanceolate, abruptly attenuate, densely tomentose; otherwise similar to the species.

Distribution: western Montana, Wyoming, and Idaho.

MONTANA: hills, "Snowshoe Gulch," July 12, 1883, *Canby 189* (Ph).

WYOMING: eastern slopes of the Big Horn Mts., headwaters of Clear Creek, Johnson Co., alt. 7000–9000 ft., July 20–Aug. 15, *Tweedy 3151* (NY, RM); headwaters of the Tongue River, Big Horn Mts., July, 1898, *Tweedy 10* (NY TYPE); Big Horn Mts., Sheridan Co., alt. 7500 ft., July, 1899, *Tweedy 214* (NY).

IDAHO: hillsides, Craig Mt. at Lake Waha, Nez Perces Co., May 24, 1892, *Sandberg, MacDougal & Heller 248* (M).

The subentire to incised leaf-blades, the tomentose-pubescent leaves, and the linear-lanceolate, strongly attenuated and acute bracts are the main distinguishing characters of this variety.

10. Balsamorhiza macrophylla Nutt. in Trans. Am. Phil. Soc. II, **7**: 350. 1841; Torr. & Gray, Fl. N. Am. **2**: 301. 1842; Walp. Rep. Bot. Syst. **2**: 610. 1843; Gray, Syn. Fl. N. Am. **1**^{2}: 266.

1884; Rydb. Fl. Rocky Mts., ed. 2, 929. 1922; Blake in Contr. U. S. Nat. Herb. [Tidestrom's Fl. Utah & Nevada] **25**: 583. 1925.

Balsamorhiza macrophylla var. *terebinthacea* Nels. in Coult. & Nels. Bot. Rocky Mts., 546. 1909, not *B. terebinthacea* (Hook.) Nutt.

Stems subscapose, 3–10 dm. high, crisp-pilose and glandular to glabrate; leaves pinnate or pinnately cleft, rarely subentire, 3–6 dm. long, 6–16 cm. broad, hirsute-ciliate on the margins, above green and sparsely crisp-hirsute to glabrous, beneath green, glandular, and crisp-hirsute on the veins, segments 5–11 cm. long, entire or sparsely toothed; petioles glandular, glabrous to sparingly pubescent; heads solitary, including the rays 8–12 cm. broad; bracts of the involucre lanceolate, oblong-lanceolate, 2.5–5 cm. long, acute to acuminate, densely pilose to hirsute-pilose-ciliate, dorsal surface sparsely pilose-hirsute; rays broadly oblong-elliptical, 3.5–5.5 cm. long, 1.5–2.2 cm. broad, bifid or entire, tube and outer surface of lamina puberulent or glabrous; achenes linear-oblong, quadrangular, with a small rib between each of the larger angles, 8–10 mm. long, glabrous.

Distribution: dry open slopes and sage-brush associations, western Wyoming and eastern Idaho, south to northern Utah.

Idaho: mountain meadows, Lake Henry, Fremont Co., July 15, 1899, *Blankinship* (M, RM); dry soil, Victor, Fremont Co., July 11, 1901, *Merrill & Wilcox 998* (G, NY, RM); Beaver Creek Canyon, Fremont Co., June 28, 1890, *Rydberg* (NY); Beaver Creek Canyon, Fremont Co., June 27, 1895, *Shear 3037* (NY); hills, Beaver Creek Canyon, Fremont Co., June 27, *Shear 3008* (NY); dry open slopes, Caribou Mts., Bonneville Co., July 17, 1923, *Payson & Armstrong 3507* (G, M, RM, Ph); Oxford, Oneida Co., May 9, 1885, *Leonard* (G).

Wyoming: Union Pass, Wind River Mts., Fremont Co., Aug. 10, 1894, *Nelson 4015* (RM); sagebrush slopes, 20 mi. east of Big Piney, Sublette Co., July 9, 1922, *Payson & Payson 2605* (G, M, Ph, RM, U CAL, NY); headwaters of the Hoback River, Lincoln Co., alt. 8000 ft., July 18, 1933, *Williams 1317* (M); Gros Ventre Mts., Teton Co., alt. 8500 ft., Aug. 29–Sept. 6, 1900, *Curtis* (NY).

Utah: Parley's Cañon near Salt Lake City, Salt Lake Co., alt. 8000 ft., July 1, 1898, *Jones 6407* (M); Parley's Canyon near Salt Lake City, June 23, 1922, *Osterhout 6212* (RM); Ft. Douglas, Salt Lake Co., May 5, 1908, *Clemens* (Ph); Red Butte, April 24, 1908, *Clemens* (G, M); Red Rock Canyon, Salt Lake Co., June 11, 1905, *Rydberg 6082* (NY, RM); Wasatch Mts., alt. 5000 ft., May, 1869, *Watson 597* (G, NY); South Weber, Weber Co., May 31, 1917, *Jones 487* (G); Lewiston to

Club River, May 8, 1911, *Smith 2366* (NY); Midway, Wasatch Co., June 15, 1933, *Eastwood & Howell 507* (M).

10a. var. **idahoensis** W. M. Sharp, var. nov.[13]

Leaf-segments 3–6 cm. long, 1–2.5 cm. broad, coarsely serrate-dentate or incised, acute, uniformly crisp-pilose to pilose-tomentose on both surfaces; petioles pilose-tomentose; bracts of the involucre usually shorter than the disk, lanceolate, 1–2 cm. long, pilose to pilose-tomentose; in all other characters similar to the species.

Distribution: known only from Boise Co., western Idaho.

IDAHO: rocky ground, Squaw Creek, Boise Co., alt. 3500 ft., May 8, 1911, *Macbride 820* (F, G, M TYPE, NY, RM, U CAL).

The variety *idahoensis* may be distinguished from the species *Balsamorhiza macrophylla* by the smaller and shallowly incised leaf-segments, the uniformly pilose leaf-surface, the pilose-tomentose petioles, and the short involucral bracts.

11. Balsamorhiza serrata Nels. & Macbr. in Bot. Gaz. **56**: 479. 1913.

Stems scapose, unbranched, 1–3.5 dm. high, crisp-pilose, with hirsute-hispidulous hairs intermixed; leaves chiefly basal, lanceolate to ovate-lanceolate, 0.6–3 dm. long, 2–10 cm. broad, dentate- to serrate-subuliferous, acute, strigose to hispidulous on both surfaces, interspersed with minute stiff hairs, conspicuously reticulate-veined, coriaceous; heads solitary, 5–8 cm. broad including the rays; bracts of the involucre linear-lanceolate, about as long as the disk, subuliferous, tomentose to crisp-pilose, herbaceous; rays yellow, oblong, 2.5–3.5 cm. long, 6–8 mm. broad, bidentate, tube and outer surface of lamina hirsutulous to glabrate; achenes linear-oblong, 6–7 mm. long, glabrous, epappose.

Distribution: dry rocky ground, Columbia Co., Washington, to Morrow and Wasco Counties, south to Harney and Lake Counties, Oregon.

[13] **B. macrophylla** var. **idahoensis** W. M. Sharp, var. nov., segmentis folii 3–6 cm. longis, 1–2.5 cm. latis, serrato-dentatis vel incisis, acutis, utrinque piloso-crispis vel piloso-tomentosis; petiolis piloso-tomentosis; bracteis involucri disco brevioribus, lanceolatis, 1–2 cm. longis, pilosis vel piloso-tomentosis. Cetera speciei similis.—Collected on rocky ground, Squaw Creek, Boise Co., Idaho, alt. 3500 ft., May 8, 1911, *Macbride 820* (F, G, M TYPE, NY, RM, U CAL).

WASHINGTON: Blue Mts., Columbia Co., July 9, 1913, *Darlington 54* (G, RM).

OREGON: Union Co., 1887, *Cusick 595, 1031* (G); upper Tygh Valley, Wasco Co., April 23, 1933, *Bellinger* (WU); dry ground near Shaniko, Wasco Co., May 5, 1928, *Gale 100* (M); dry stony ground, 10 mi. north of Wapinitis, Wasco Co., May 29, 1933, *Peck 17393* (WU); rocky hills near Rock Creek, Morrow Co., alt. 1090 m., May 19, 1894, *Leiberg 83* (G, M, NY, RM TYPE); near Rhea Creek, vicinity of Lexington, Morrow Co., alt. 605 m., May 12, 1894, *Leiberg 58* (F, G, M, NY, RM); John Day Valley, May 16, 1885, *Howell* (F, G, NY, Ph); dry rocky mountain top near Fossel, Wheeler Co., June 3, 1925, *Henderson 5248* (G); mesa, between Warner Valley P. O. and Big Lake, Lake Co., alt. 1600 m., June 16, 1911, *Eggleston 6964* (NY); dry sterile soil, Lakeview, Lake Co., June 27, 1927, *Peck 15264a* (M, WU); stony flat on Stein's Mts., Harney Co., June 30, 1898, *Cusick 1984* (F, G, M, U CAL); Silver Creek meadows, 6 mi. west of Ripley, Harney Co., June 22, 1925, *Peck 13900* (WU); near Harper Ranch, alt. 1000 m., May 22, 1896, *Leiberg 2106* (G, NY, U CAL).

12. **Balsamorhiza hispidula** W. M. Sharp, sp. nov.[14]

Stems 0.6–3 dm. high, pilose-hirsute, glandular; leaves 1–4 dm. long, pinnately divided, the segments unequally pinnately cleft or parted, 2–4.5 cm. long, acute, green on both surfaces, above sparsely hispid, hispid-pilose to hispidulous, glandular, beneath globular-resinous and usually hispid, hispidulous or hispid-pilose on the veins; petioles pilose-hirsute to pilose-hispid, glandular; heads radiate, solitary, 4.5–6 cm. long including the rays; bracts of the involucre linear to linear-lanceolate, about as long as the disk, the outer series as long as or longer than the inner series, more or less pilose-hirsute-ciliate, acute to acuminate, the outer surface interspersed by numerous glands; rays yellow, bidentate, 2.5–3 cm. long, tube and outer surface of lamina hirtellous; achenes 6–7 mm. long, glabrous, epappose.

Distribution: dry grounds, southwestern Wyoming, Idaho and northern Utah, west to Nevada.

WYOMING: South Butte, "thirteen mile," July 17, 1897, *Nelson 3552* (RM).

IDAHO: vicinity of Pocatello, Bannock Co., 1921, *Soth 7* (NY); hills near Oxford,

[14] B. hispidula W. M. Sharp, sp. nov., caulibus 0.6–3 dm. altis, piloso-hirsutis et glandulosis; foliis 1–4 dm. longis pinnatisectis, segmentis inaequaliter pinnatifidis vel pinnatipartitis, 2–4.5 cm. longis, acutis, utrinque viridibus, supra sparse hispido-pilosis vel hispidulis et glandulosis, subtus globuloso-resinosis et plerumque hispidis, in nerviis hispidulis vel hispido-pilosis; petiolis piloso-hirsutis vel piloso-hispidis, glandulosis; bracteis involucri disco aequalibus, linearibus vel lineari-lanceolatis, plus minusve piloso-hirsuto-ciliatis et glandulosis, acutis vel acuminatis.—Collected at Lake Point, Tooele Co., Utah, alt. 4300 ft., May 20, 1880, *Jones 1727* (F, NY, RM, U CAL TYPE).

Bannock Co., May 16, 1885, *Leonard 45* (NY); gravelly waste ground, Twin Falls, Twin Falls Co., May 9, 1912, *Bennitt* (RM).

UTAH: Big Cottonwood Canyon, vicinity of Salt Lake City, May 23, 1908, *Clemens* (F, Ph); Fort Douglas, Salt Lake Co., May 5, 1908, *Clemens* (F); vicinity of Salt Lake City, Salt Lake Co., 1883, *Meehan* (M, Ph); Garfield, Salt Lake Co., alt. 4300 ft., May 30, 1884, *Leonard 66* (G, NY); west of Taylorsville, Salt Lake Co., May 4, 1916, *Jones 314* (G); Murray, Salt Lake Co., May 10, 1915, *Jones* (U CAL); Antelope Is., Davis Co., alt. 5500 ft., June, 1869, *Watson 596* (NY, G); western slopes of the Wasatch Range, Springville, Utah Co., alt. 4400–5000 ft., May 17, 1913, *Hill* (M); Tintic, Juab Co., May 16, 1891, *Jones* (M, U CAL); Lake Point, Tooele Co., alt. 4300 ft., May 20, 1880, *Jones 1727* (F, NY, RM, U CAL TYPE); "Hugway," May 29, 1891, *Jones* (NY); St. George, Washington Co., 1877, *Palmer 236* (F, G, M, NY).

NEVADA: Pinon-Juniper Assoc., 3 mi. west of Baker, White Pine Co., alt. 6500 ft., June 16, 1933, *Maguire & Becraft 2840* (M); 1891, *Jones* (M); Emigrant Pass, Eureka Co., June 10, 1933, *Eastwood & Howell 203* (M).

13. **Balsamorhiza hirsuta** Nutt. in Trans. Am. Phil. Soc. II, **7**: 349. 1841; Torr. & Gray, Fl. N. Am. **2**: 301. 1842; Walp. Rep. Bot. Syst. **2**: 610. 1843; Gray, Syn. Fl. N. Am. **1**^{2}: 266. 1884; Howell, Fl. Northwest Am. **1**: 340. 1900; Piper in Contr. U. S. Nat. Herb. [Fl. State Wash.] **11**: 581. 1906; Rydb. Fl. Rocky Mts., ed. 2, 929. 1922, in part; Blake in Contr. U. S. Nat. Herb. [Tidestrom's Fl. Utah & Nevada] **25**: 583. 1925, in part; Jepson, Manual Fl. Pl. Cal. 1078. 1925, in part.

Balsamorhiza Hookeri var. *hirsuta* (Nutt.) Nels. in Coult. & Nels. Bot. Rocky Mts. 546. 1909.

Stems subscapose, 1.5–4.5 dm. high, hirsute to hirsute-pilosulous, and glandular; leaves lanceolate to oblong-lanceolate, pinnately divided, 1.5–4.5 dm. long, the divisions pinnatisect or bipinnatisect, 2.5–6 cm. long, .5–2.5 cm. broad, the ultimate segments linear to lanceolate, acute, both surfaces green, strigose-hirsute, and glandular; petioles strigose-hirsute; heads solitary, radiate, 5–9 cm. broad including the rays; bracts of the involucre 3–4-seriate, erect or somewhat spreading, ovate-attenuate to an acute apex, as long as or shorter than the disk, pilose-ciliate, hirsute; rays yellow, oblong-lanceolate, 2.5–4 cm. long, 7–8 mm. broad, bifid or entire, tube and outer surface of lamina pubescent; disk-corollas 8–9 mm. long, the limb hirsutulous; achenes linear-oblong, 5–6 mm. long, glabrous.

Distribution: dry open grounds, southeastern Washington to northeastern Oregon.

WASHINGTON: east of Walla Walla, Walla Walla Co., 1834, *Nuttall* (G, TYPE collection).

OREGON: summit of Cabbage Hill, east of Pendleton, Umatilla Co., June 14, 1928, *Thompson 4863* (G, M); dry ground, Hot Lake, Union Co., May 19, 1923, *Sherwood 363* (F, WU); Hot Lake, Union Co., May 19, 1923, *Sherwood 268* (WU); dry rocky hillsides, Union Co., alt. 3500 ft., June–July, 1881, *Cusick 441* (F, G); northeastern Oregon, May 20, 1898, *Cusick 1872* (F, G, M, RM, U CAL); stony ridge, "mouth of Ladd Canyon," northeastern Oregon, June 7, 1898, *Cusick 1921* (F, G, M, U CAL).

13a. var. **lagocephala** W. M. Sharp, var. nov.[15]

Stems 0.6–2.5 dm. high, pilose, intermixed with numerous short hairs; leaves pinnately cleft or divided, 1–2 dm. long, the divisions 1–2 cm. long, 0.5–1.5 cm. broad, cleft into three or more ascending, acute lobes, hirsute on both surfaces, often densely interspersed with glands; bracts of the involucre lanceolate, shorter than the disk, the outer series progressively shorter than the inner series, acute, densely tomentose or pilose-tomentose, especially towards the base of the involucre; in other characters similar to the species.

Distribution: rocky sagebrush habitats in Lincoln, Grant, and Kittitas Counties of central Washington.

WASHINGTON: Davenport, Lincoln Co., alt. 2500 ft., May 20, 1905, *Jones* (NY); rocky hillside, Ephrata, Grant Co., April 13, 1924, *St. John, Pickett, Cary & Warren 6314* (Ph); rocky sagebrush plains near Coulee City, Grant Co., May 2, 1931, *Thompson 6163* (G); "Rimrock scabland," north of Ellensberg, Kittitas Co., April 23, 1932, *Thompson 8229* (M TYPE, NY); sandy soil, Ellensberg, Kittitas Co., May 20, 1897, *Piper 2718* (G); sage-brush slopes near Vantage, Kittitas Co., April 23, 1932, *Thompson 8212* (NY, RM).

13b. var. **neglecta** W. M. Sharp, var. nov.[16]

Leaf-segments linear-lanceolate to lanceolate, 2–4 cm. long,

[15] **B. hirsuta** var. **lagocephala** W. M. Sharp, var. nov., caulibus 0.6–2.5 dm. altis, pilosis et hispidulis; foliis pinnatifidis vel pinnatisectis, 1–2 dm. longis, segmentis 1–2 cm. longis, 0.5–1.5 cm. latis, adscendentibus, acutis, utrinque hirsutis, saepe glandulosis; bracteis involucri lanceolatis, disco brevioribus, exterioribus interiorbus plus minusve brevioribus, acutis, dense tomentosis vel piloso-tomentosis, praesertim ad basem involucri. Cetera speciei similis.—Collected at "Rimrock scabland," north of Ellensberg, Kittitas Co., Washington, April 23, 1932, *Thompson 8229* (M TYPE, NY).

[16] **B. hirsuta** var. **neglecta** W. M. Sharp, var. nov., segmentis folii lineari-lanceolatis vel lanceolatis, 2–4 cm. longis, 1–1.5 cm. latis, integris vel pinnatisectis, adpresso-hirsutis; bracteis involucri disco aequalibus, linearibus vel anguste lineari-lanceolatis, dense piloso-tomentosis vel tomentosis. Cetera speciei similis.—Collected at Truckee Pass, Washoe Co., Nevada, alt. 4450 ft., May 1, 1909, *Heller 9592* (F TYPE, G, NY, Ph).

1–1.5 cm. broad, entire to pinnately parted, appressed-hirsute; bracts of the involucre about as long as the disk, linear to narrowly linear-lanceolate, densely pilose-tomentose to tomentose; in all other characters similar to the species.

Distribution: dry grounds, northeastern Utah west to Washoe Co., Nevada.

UTAH: Sheep Creek Canyon, Daggett Co., June 4, 1932, *Williams 520* (NY, RM); near Fort Duchesne, Uinta Co., 1913, *Carter 4* (RM).

NEVADA: Truckee Pass, Washoe Co., alt. 4450 ft., May 1, 1909, *Heller 9592* (F TYPE, G, NY, Ph); Trinity Mts., Humboldt Co., May, 1868, *Watson 595* (G, NY); near Carson City, Ormsby Co., 1864, *Anderson 69* (G); north of Carson City, May, 1865, *Stretch 156* (NY).

14. **Balsamorhiza terebinthacea** (Hook.) Nutt. in Trans. Am. Phil. Soc. II. 7: 349. 1841; Walp. Rep. Bot. Syst. 2: 610. 1843; Gray in Mem. Am. Acad. [Pl. Fendl.] N. S. 4: 82. 1848, in part; Gray, Syn. Fl. N. Am. 1^2: 266. 1884; Howell, Fl. Northwest Am. 1: 340. 1900; Piper in Contr. U. S. Nat. Herb. [Fl. State Wash.] 11: 581. 1906; Rydb. Fl. Rocky Mts., ed. 2, 929. 1922, in part.

Heliopsis (?) *terebinthacea* Hook. Fl. Bor.-Am. 1: 310. [1834] 1840; DC Prodr. 5: 551. 1836.

Stems subscapose, 2.5–5 dm. tall, crisp-hirsute or crisp-pilose, glandular; leaves lanceolate or oblong-lanceolate, thick, 2–4 dm. long, 5–10 cm. broad, pinnately cleft or parted, the lobes sparsely dentate-serrate or entire, acute, strigose-hirsute on both surfaces; heads solitary, 4–6 cm. broad including the rays; bracts of the involucre linear-lanceolate to ovate-lanceolate, about as long as the disk, acute, crisp-pilose to crisp-hirsute, herbaceous; rays yellow, oblong-cuneate, 2.5–3.5 cm. long, 6–9 mm. broad towards the apex, tube and outer surface of the lamina pubescent; achenes 7–8 mm. long, glabrous, epappose.

Distribution: southwestern Washington, south to Siskiyou County, California.

WASHINGTON: low ground in open pine woods, Falcon Valley, Klickitat Co., June 17, 1922, *Suksdorf 10866* (G, M, NY, Ph, U CAL); Klickitat River, May 18, 1884, *Suksdorf 360* (G); low grounds in pine woods, Falcon Valley, *Suksdorf 135* (G); foothills of Cascade Mts., Yakima Region, 1882, *Brandegee 96* (M, U CAL); near Fort Vancouver, "1825," *Douglas* (K TYPE).

OREGON: dry stony slope, 12 mi. west of Waldo, Josephine Co., July 2, 1918, *Peck 8456* (WU).

CALIFORNIA: Shasta Valley, Siskiyou Co., May 10, 1910, *Butler 1337* (U CAL).

GREENMANIELLA W. M. Sharp

Greenmaniella W. M. Sharp, gen. nov.[1]

Perennial suffruticose plants with alternate ovate leaves. Heads heterogamous, medium-sized, disposed in subcorymbose clusters. Involucral bracts 2–3-seriate, the outermost series herbaceous or subherbaceous, the two inner series membranaceous, marked by six or more brownish-resinous parallel nerves. Receptacle narrowly conical; pales concave to semiconduplicate, membranaceous with several brownish resinous parallel nerves. Ray-flowers styliferous and fertile, rays light yellow; disk-flowers fertile, tube narrowly cylindrical, the base narrowed and seated inside the cup-like crown of the achene, limb campanulate, 5-lobed. Anther appendages ovate, base subsagittate; style-branches recurved, obtuse or acute, pubescent towards the apex. Achenes subfusiform, broadly subangulate, sparsely carunculate. Pappus a shallow cup-like crown, with knob-like projections at the angles.

Greenmaniella resinosa (Watson) W. M. Sharp, comb. nov.

Zaluzania resinosa Watson in Proc. Am. Acad. **25**: 153. 1890; Rob. & Greenm. in Proc. Am. Acad. **34**: 533. 1899.

Plants suffrutescent, 1.5–2.5 m. tall; stems branched above, sulcate, pilose-tomentulose; leaves ovate, 0.5–3 dm. long, 2–14 cm. broad, serrate-mucronate, acuminate, acute at the base, triple-veined, substrigose-hirsute above, subpilose on the veins below, interspersed by numerous resinous globules; heads 6–8 mm. high.

[1] **Greenmaniella** W. M. Sharp, gen. nov. Capitula heterogama, radiata, floribus radii uniseriatis et floribus disci fertilibus. Involucrum subcampanulatum, bracteis 2–3-seriatis, exterioribus herbaceis, interioribus submembranaceis striatisque. Receptaculum anguste conicum, paleis concavis vel subconduplicatis, membranaceis striatisque marginibus plus minusve scariosis. Corollae radii ligulae patentes, integrae, apici dentatae. Corollae disci tubulo-campanulatae, regulares, tubo basi non dilatato, limbo late campanulato 5-dentato. Antherae basi subsagittatae, apici appendiculatae. Styli rami complanati, elongati, obtusi vel acuti. Achenia disci subfusiforma, subtetragona, breve coronata.—Plantae verisimilliter suffruticosae, foliis alternatis.

Distribution: Nuevo Leon in the Sierra Madre near Monterey, Mexico.

MEXICO: NUEVO LEON—Sierra Madre, near Monterey, Aug. 24, 1889, *Pringle 2412* (F, G TYPE, M, U CAL, US); Sierra Madre, above Monterey, 3000 ft. alt., Aug. 25, 1903, *Pringle 11615* (F, G, US); Sierra Madre, "Conquor," near Monterey, July 9, 1888, *Pringle 2222* (G); vicinity of Monterey, 750 m. alt., Aug. 1911, *Arsène 6176* (M).

LIST OF EXSICCATAE

The collectors' numbers are indicated by *italics;* the collections without numbers are indicated by a dash. The numbers in parentheses refer to the species number used in this monographic study. The genus, in each case, precedes its list of exsiccatae.

BALSAMORHIZA

Abrams, L. R., & E. A. McGregor. *356, 833* (4).
Anderson, C. L. *69* (13b).
Anderson, F. W. — (5).
Austin, R. M. *94, 47* (5);—, — (7).
Austin, R. M. & Bruce. *2179* (7).
Ayres, W. B. *63* (5).
Baker, C. F. *51, 926* (5).
Baker, M. S. & F. P. Nutting. —(7).
Bellinger, G. C. — (11).
Bennitt, D. *28* (12).
Bigelow, J. M. — (4); — (8).
Blankinship, J. W. — (4); *52* (5); — (10).
Bolander, H. N. *4526* (2); *6187* (5).
Brandell, E. M. — (4).
Brandegee, K. — (1); — (4); *208* (8); *2469* (8).
Brandegee, T. S. — (1); *891* (3); —, — (4); *1077* (5); *96* (11).
Butler, G. D. *1180, 595* (4); *1157* (6b); *1337* (14).
Canby, W. M. *189* (9a).
Carter, W. R. — (4); *4* (13b).
Chandler, H. P. *914* (8).
Clark, J. A. *28* (5).
Clemens, Mrs. Jos. — (5); —, — (10); —, — (12).
Congdon, J. W. —, — (2); — (8).
Cooper, R. D. *1182* (5).
Cotton, J. S. *1105, 1052, 976* (3); *336* (4); *568* (6a).
Crandall, C. L. *2723* (5).
Culbertson, J. W. *4413* (1).
Curtis, C. C. — (10).
Cusick, W. C. *595, 3255, 1679, 3332,* (3); *1984* (11); *441, 1872, 1921* (13).
Darlington, H. T. *54* (11).
Davidson, A. *2058* (1).
Davy, J. B. *2185* (4).
Douglas, D. — (14).
Drake & Dickson. — (4).
Drew, E. R. — (7).
Dudley, W. B. *363* (4).
Eastwood, A. *11927, 3237* (4); *896* (7).
Eastwood, A. & T. Howell. *203* (12); *507* (10).
Eggleston, W. W. *6820* (4); *6964* (11).
Elmer, A. D. E. *4374* (8).
Engelmann, G. — (5).
Ferris, R. S. *1580* (4).
Gabrielson. — (5).
Gale, N. P. *111* (4); *178*, — (9); *100* (11).
Gardner, N. S. — (4).
Gorman, M. W. — (4).
Grant, J. M. —(4).
Greene, E. L. — (2); *718* (4); *745* (6b).
Griffiths, D. & J. S. Cotton. *483* (3).
Griffiths, D. & B. Hunter. 77 (9).
Hall, E. *276* (4).
Hall, H. M. *6263, 8907, 11246, 7797* (4); *1032* (7); *8885* (8).
Hall, H. M. & G. R. *8340* (1).
Hall, H. M. & H. D. Babcock. *5100* (4).

Hall, H. M. & H. P. Chandler. *7304* (4).
Hammond, E. W. *209* (4).
Hansen, G. *168* (2); *420* (5); *1069* (8).
Hayden, F. V. —, — (9).
Heller A. A. *11977*, *7802* (4); *14594*, *12026* (5); *9592* (13b).
Heller, A. A. & E. G. *2958* (5); *3298* (9).
Henderson, L. F. *362*, *5902* (4); *5703* (7); *5248* (11).
Hill, G. R. — (12).
Holmes, F. — (4).
Horner, R. M. *B277* (5); — (9).
Howell, T. J. —, — (4); —, —, — (6); — (7); — (11).
Jack, J. G. — (9).
Jones, A. J. — (12).
Jones, M. E. — (3); *6407* (10); —, *1727*, — (12); — (13a).
Jones, W. W. *487* (8); — (9); —, *314* (12).
Kammerer, A. L. *60* (4).
Kellogg, A. & W. G. W. Harford. *430* (8).
Kelsey, F. D. — (5).
Kennedy, P. B. *1985* (5); *1859* (13a).
Kirkwood, J. E. *1732* (5).
Konger, K. *127843* (8).
Leiberg, J. B. *142*, *28* (3); — (5); *114* (5); *2106*, *83*, *58* (11).
Leonard, F. E. — (10); *66*, *45* (12).
Lloyd, F. E. — (10).
Lunell, J. *67* (4).
Lyall, D. — (4).
Macbride, J. F. *202*, *79* (5); *820* (10a).
Macoun, J. *86299*, *76941*, *953* (4); —, *76942* (5).
Maguire, B. & R. J. Becraft. *2840* (12).
Meehan, T. — (12).
Merrill, E. D. & E. N. Wilcox. *686* (5); *743* (9); *998* (10).
Mooney, W. T. — (6b).
Moore, C. H. — (5).
Murdock, J. *4096* (5).
Nelson, A. *7084*, *9140*, *4518* (5); *2342* (9); *4015* (10); *3552* (12).
Nelson, A. & E. *5613* (5).
Nelson, E. *1476* (4); *1595* (6); *4993* (9).
Nelson, J. C. *1091*, *3506* (4).
Newcombe, C. F. *62* (4).
Nuttall, T. — (4); — (5); — (6); — (9); — (12).
Osterhout, G. E. *6212* (10).
Page, E. B. *216* (4).
Palmer, E. J. — (5); *236* (12).
Pammel, L. H. *75* (5).
Pammel, L. H. & E. M. Stanton. *322* (9).
Parry, C. C. *165* (9).
Payson, E. B. *343* (5).
Payson, E. B. & L. B. *2605* (10).
Payson, E. B. & G. M. Armstrong. *3507* (10).
Peck, M. E. *5040*, *13249*, *3069* (4); *15544*, *3071* (5); *13900*, *15264*, *17393* (11); *8456* (14).
Piper, C. V. — (3); —, *4945* (4); *1594* (5); *2718* (15a).
Prescott, H. S. *11* (4).
Ramaley, F. *11109* (10).
Rich, Maj. — (2).
Rydberg, P. A. *808* (5); —, *6082* (10).
Rydberg, P. A. & E. A. Bessey. *5174* (5); *5175* (9).
St. John, H. & R. H. Brown. *3900* (9).
St. John, Pickett, Cary & Warren. *6314* (13a).
Sandberg, J. H. & J. B. Leiberg. *166*, — (3); *573* (4); *23* (5).
Sandberg, J. H., D. T. MacDougal & A. A. Heller. *248* (9); *248* (9a).
Schmoll, H. M. & D. Nusbaum. *1574* (5).
Sharp, S. S. *356* (5).
Shear, C. L. *3037*, *3009* (10).
Sherwood, W. *372* (5); *323* (9); *268*, *363* (13).
Smith, C. P. *2348* (5); *2366* (10).
Sonne, C. F. *368*, — (7).
Soth, M. E. *7* (12).
Spalding, — (3); — (9).
Stretch, *156* (13b).
Suksdorf, W. N. *364*, —, — (4); *357*, —, *363*, *359* (6); *10866*, *360*, *135* (14).

Thompson, J. W. *5171* (3); *5133, 561, 2495, 2593, 2163* (4); *6126, 6386, 5985* (5); *227* (7); *4863* (13); *6163, 8229, 8212* (13a).
Torrey, J. — (2); — (8).
Tracy, J. P. *4175, 6662, 6984* (4).
Tweedy, F. *2115, 11, 3150* (9); *214, 10, 3151* (9a).
Umbach, L. M. *60* (5).
Walker, E. P. *466* (5).
Walker, H. A. *1285* (4); *2016* (5).
Warren, E. D. — (5).
Watson, S. *596* (12); *597* (10); *595* (13b).
Williams, L. *1125, 415* (5); *1317* (10); *520* (13b).
Williamson, J. W. *185* (4).
Zeller, S. M. — (4).

ECHINACEA
Bartholomew, E. — (3).
Biltmore, Herb. *1107* (3a).
Blakley, O. W. *1436* (4).
Buckley, S. B. — (2).
Burk, M. *772* (4).
Bush, B. F. —, —, *26, 6146* (1); *38, 149, 156, 261* (4); *42, 76, 155* (5).
Carr, W. P. *90* (3).
Chase, V. H. *685* (1); *642* (4).
Churchill, J. R. — (4).
Clemens, Mrs. Jos. *11837* (3).
Clemens, Mr. & Mrs. Jos. *381* (3).
Clothier, G. L. — (3).
Curtiss, A. H. *3502* (2).
Davis, J. *4864, 1574, 3284, 1844, 5819* (1); *4185, 4405* (4).
Dewart, F. W. — (4).
Earle, F. S. — (1).
Eggert, H. —, — (1); — (3); —, — (3a); —, —, —, —, —, — (4).
Engelmann, G. — (3).
Fisher, G. L. — (4).
Gattinger, A. — (3a).
Glatfelter, N. M. *275*, — (1); — (3).
Goodding, L. N. *2215* (3).
Graves, — (4).
Greenman, J. M. *4007* (1); *412* (4).
Hall, E. *330* (4).
Harper, R. M. *1884* (1).
Hedgcock, G. G. — (4).
Heller, A. A. *1735, 13984* (3).
Hitchcock, A. S. — (4).
Houghton, H. W. *3642* (5).
House, H. D. *2206* (2).
Kearney, T. H. — (1).
Kellogg, J. H. —, *438* (4).
Larsen, E. L. *198* (3).
Lettermann, G. W. — (1); — (4).
Lindheimer, F. *898* (3).
Mackenzie, K. K. *64, 373* (1).
Mathias, M. E. — (1).
Meade, S. B. *1841* (1).
Murrill, W. A. — (2).
Nelson, A. *2122, 8546* (3); — (4).
Norton, J. B. S. *265* (3).
Palmer, E. J. *32445, 42569, 5843* (1); *37546* (3); *178, 1206, 5783, 7632, 8061, 18088, 18016, 34749, 69853* (4); *5844, 9617, 30397, 34714* (5).
Pammel, L. H. *243* (4).
Pammel, L. H. & Stanton, *247* (3).
Price, S. F. — (4).
Reverchon, J. —, *2579* (4).
Rose, G. M. — (3).
Russell, C. — (1).
Ruth, A. *243, 646* (5).
Rydberg, P. A. & R. Imler. *400* (4).
Stephenson, B. C. — (1).
Stevens, G. W. *737, 971, 1341K* (3).
Sykes, D. — (3).
Thornber, J. J. — (3).
Tracy, S. M. *8331* (4).
Warner, S. R. — (4); — (5).
Webber, H. J. — (3).
White, — (4).
Williams, T. A. — (3).
Wislizenus, A. *196* (4).
Zeller, C. — (3).

GREENMANIELLA
Arsène, G. *6176* (1).
Pringle, C. G. *2222, 2412, 11615* (1).

IOSTEPHANE
Arsène, G. *2464, 5518* (1); *1056* (1a).
Arsène, G. & Nicolas. *5408* (1).
Bourgeau, E. *602* (1).
Coulter, Thomas. *374* (1a).
Conzatti, C. & V. Gonzalez. *404* (1a).
Ehrenberg, C. *344* (1a).
Ghiesbreght, A. *101, 561* (2).
Holway, E. W. D. *3543* (1a).
Nelson, E. W. *1371a, 3223* (2).

Palmer, E. *65* (1); *333, 4824* (1a); *372* (1b).
Parry, C. C. & E. Palmer. *470* (1a).
Pringle, C. G. *5249, 9276, 9929* (1); *4480* (1b); *4978* (2).
Purpus, C. A. *5694,* (1a); *4120, 55* (2).
Rose, J. N. *2336, 2969* (1a).
Rose, J. N. & J. H. Painter. *6493* (1).
Schaffner, J. G. *58, 253* (1).
Seaton, H. E. *366* (1a).

RATIBIDA
Anderson, J. P. — (4).
Arsène, G. *2603* (1).
Arsène, G. & A. Benedict. *15445, 15841* (2).
Baker, C. F. — (1); *667* (2).
Barlow, B. — (2).
Bebb, R. *3508* (4).
Blankinship, J. W. *283* (1).
Brandegee, T. S. *751* (1); *12051* (2).
Burk, M. *556* (4).
Bush, B. F. *157, 163, 307 1234* (1); *8407* (1a); —, *123, 164* (4).
Carr, W. P. *93* (1).
Child, M. *573* (2).
Clokey, I. W. *2819* (1); *2406* (4).
Cocks, R. S. — (3).
Crandall, C. S. — (1a).
Cratty, R. I. *1370* (4).
Davis, J. *1390, 5114, 7320* (1); — (4).
Deam, C. C. *1370* (4).
Demaree, D. *7706* (1); *7706a* (1a); *7528a* (2).
Dewart, F. W. — (1).
Drummond, T. *108* (3).
Drushel, J. R. *419* (1a).
Duncan, J. T. — (1); *28* (1a).
Earle, F. S. & E. S. *150* (2).
Eggert, H. —, —, — (1); —, — (1a); — (2); — (4).
Eggleston, W. W. — (1); *20562* (1a).
Ellis, C. C. *208* (2).
Ellis, L. D. — (1).
Emig, W. H. *366, 772* (1).
Engelmann, G. — (2).
Evans, W. H. — (2).
Fendler, A. *378* (1a); — (2).
Ferris, R. S. & C. D. Duncan. *2838* (1); *3113* (1a).
Fisher, G. L. — (1); — (1a).
Fritchey, J. Q. A. *167* (1a).
Glatfelter, N. M. — (4).
Goodman, G. J. *226* (1).
Greenman, J. M. *3624* (4).
Gregg, J. *810* (1a).
Griffiths, D. *5641* (2).
Hall, E. *336* (3a).
Hanson, H. C. *C139* (1).
Harper, R. M. *1051* (4).
Hedgcock, G. G. — (1a).
Heller, A. A. *13975, 1850* (1); *3829* (2); *1789* (3).
Hitchcock, A. S. *267* (1); *268* (2).
Johnston, E. R. *217* (1).
Jones, M. E. —, *25903* (1); *25904* (1a); *29506, 29507* (3).
Kellerman, W. A. —, — (1a).
Kramer, J. *60* (1a).
Larsen, E. L. *187* (1); *194* (1a).
Letterman, G. W. — (1); — (2); — (4).
Macoun, J. *34829* (4).
Mathias, M. E. *309, 526* (1).
Metcalf, F. P. *1896* (4).
Metcalfe, O. B. *415* (1a).
Moore, J. A. & J. A. Steyermark. *3618* (1).
Mulford, A. I. — (1); *260* (2).
Nelson, A. —, *570* (1a).
Nelson, E. W. *4777* (5).
Norton, J. B. S. & G. L. Clothier. *266* (4).
Orcutt, C. R. *5821* (1a).
Oyster, J. H. *4149* (1).
Palmer, E. *345* (1).
Palmer, E. J. *7746, 12535, 13878, 31021, 37528* (1); *7792, 8024* (1a); *12534, 31100* (2); *713* (3a); *6003, 6204, 8037, 17003* (4).
Pammel, L. H. — (1); *17* (4).
Pammel, L. H. & I. C. Ball. *56* (4).
Patterson, H. N. — (4).
Payson, E. B. *1164* (1a).
Pellet, H. L. — (4).
Poole, R. J. & D. Folsom. — (1).
Price, S. F. — (4).
Pringle, C. G. *1061* (2); *1648, 1305* (5).
Purpus, C. A. *4768* (1).

Redfield, J. H. *458* (1).
Reed, M. — (2).
Reverchon, J. *493, 3337, 3338* (1a); —, *3340* (2); *2229* (3a).
Rusby, H. H. *78* (2).
Rydberg, P. A. & R. Imler. *336* (1); *708* (2).
Shannon, J. I. *133a* (4).
Sheldon, C. S. — (1).
Sherff, E. E. *1801* (4).
Shimek, B. — (4).
Skehan, J.
Smith, J. G. & R. Pound. *145* (1a).
Standley, P. C. *5124, 5279* (1); *4926* (1a); —, *4950* (2); *5156* (2a).
Stephenson, B. C. — (4).
Stevens, G. W. *764* (1); *1080* (2); *2283* (4).
Steyermark, J. A. *1036* (4).
Stratton, R. *444, 399* (1).
Thompson, C. H. — (1); — (1a); — (2).
Thornber, J. J. —, — (1); — (1a).
Townsend, C. H. & C. M. Barber. *230* (1); *101* (5).
Tracy, S. M. *7891* (1); *8947a* (1a); *8548* (3); *8914* (3a).
Wislizenus, A. *25* (2).
Wooton, E. O. *261* (1); *247* (1a); *5* (2).
Wooton, E. O. & P. C. Standley. *3315* (1a).
Wright, C. *327* (2); — (3); —, — (3a).

ZALUZANIA

Altamirano, F. *1744* (3).
André, E. *K1243, K1245* (14).
Arsène, G. *7093* (12); *10065* (13).
Arsène, G. & Nicolas. *6162* (13).
Botteri, M. *843* (3).
Bourgeau, E. *803* (13); *385* (1); *704* (3).
Conzatti, C. *2317, 4601* (8).
Coulter, Thomas. *350* (9).
Deam, C. C. *137* (3).
Duges, A. *460* (3); —, *469* (13).
Firmin, G. *140, 471* (14).
Fisher, G. L. *136* (3).
Goodding, L. N. *864* (5).
Gregg, J. *447, 631* (4).
Hartweg, T. *111* (1a).
Holway, E. W. D. *5347* (8); *948* (14).
Kirkwood, J. E. *67, 227* (4); *129* (11).
Lemmon, J. G. —, —, —, *2764* (5).
Lloyd, F. E. *124* (4); *32* (11).
Lyonnet, P. E. *387* (9).
Mille, L. *568, 569* (14).
Nelson, E. W. *3930, 4520* (4); *4727, 4970* (7).
Orcutt, C. R. *4139* (1); *3902, 4131* (3).
Pachano, A. *134* (14).
Palmer, E. *307* (1a); *757* (3); *279, 360, 435, 592* (4); *734* (10); *314* (11).
Parry, C. C. *446* (11).
Parry, C. C. & E. Palmer. *527* (1); *445* (3).
Pittier, H. *452* (12).
Pringle, C. G. *2925, 3204, 7440, 9395, 13092* (1); *8914* (1a); *5156, 7367* (2); *9481, 13093* (3); *2402* (4); *755, 1310, 2145* (5); *8710* (6); *309, 1110* (7); *4928* (8); *6956, 7923, 9997, 13784* (9); *2398, 10076*, (10); *3144, 7451, 9996, 11614, 13091* (13).
Purpus, C. A. *77* (1); *1126, 1334* (4); *2530, 3823, 3824, 5610* (8); *2580, 3027, 4121* (12); *1539* (13).
Rose, J. N. & R. Hay. *5274, 5816* (1); *5954* (8).
Rose, J. N. & J. H. Painter. *6675* (13).
Rose, J. N., J. H. Painter & J. S. Rose. *8417* (1); *8325* (3); *7278, 8418, 9738* (13).
Schaffner, J. G. *80* (1); *345* (1a); *78* (3); *717* (4); *767* (11).
Schuman, W. *94* (3).
Seaton, H. E. *286* (12).
Smith, C. L. *612* (8).
Sodiro, A. *31/1, 31/2, 31/3* (14).
Wilcox, T. E. *469* (5).
Wislizenus, A. *189* (7).

Index to Genera and Species

New names and new combinations are printed in **bold face** type; previously published accepted names in Roman type; and synonyms in *italics*.

Explanation of Plate

PLATE 5

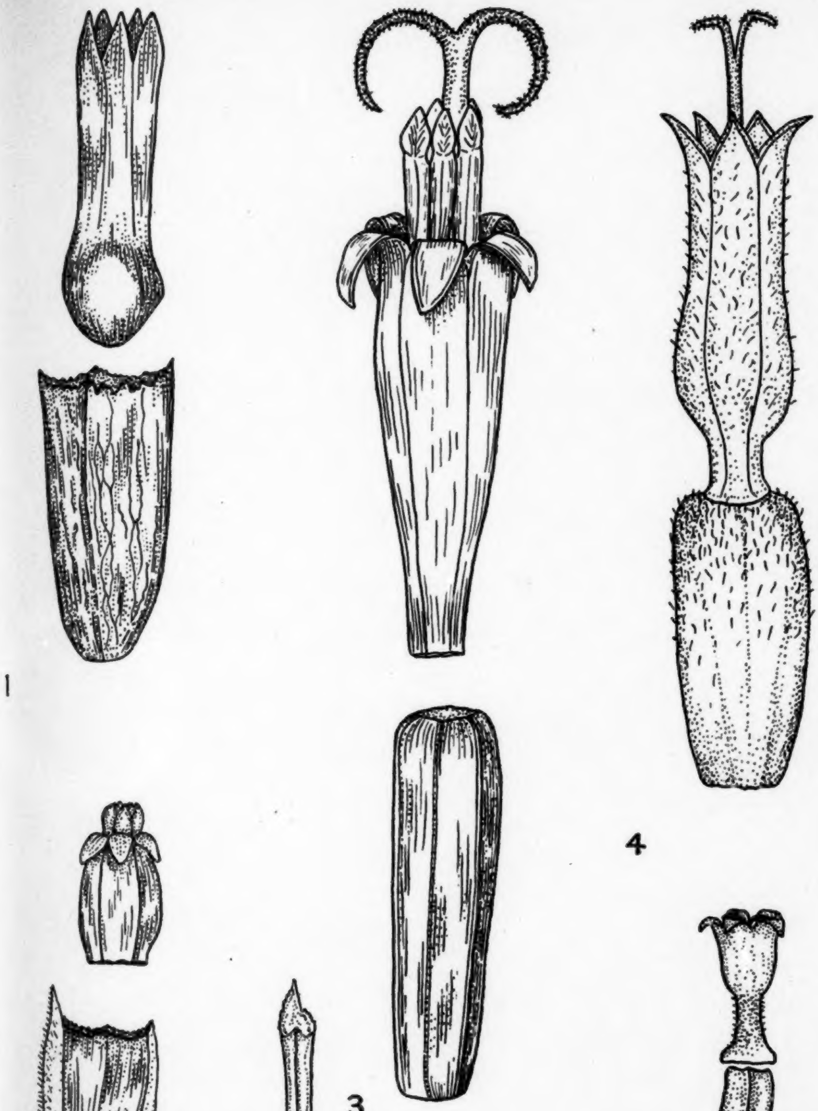
Fig. 1. Disk-flower of *Echinacea pallida*. Corolla above, achene below. × 11.

Fig. 2. Disk-flower of *Ratibida columnaris*. a. Achene, side view. b. Achene, edge view. × 9.

Fig. 3. Disk-flower of *Balsamorhiza hispidula*. Corolla above, achene below. × 9.

Fig. 4. Disk-flower of *Iostephane heterophylla*. × 7.5.

Fig. 5. Disk-flower of *Zaluzania mollissima*. × 9.



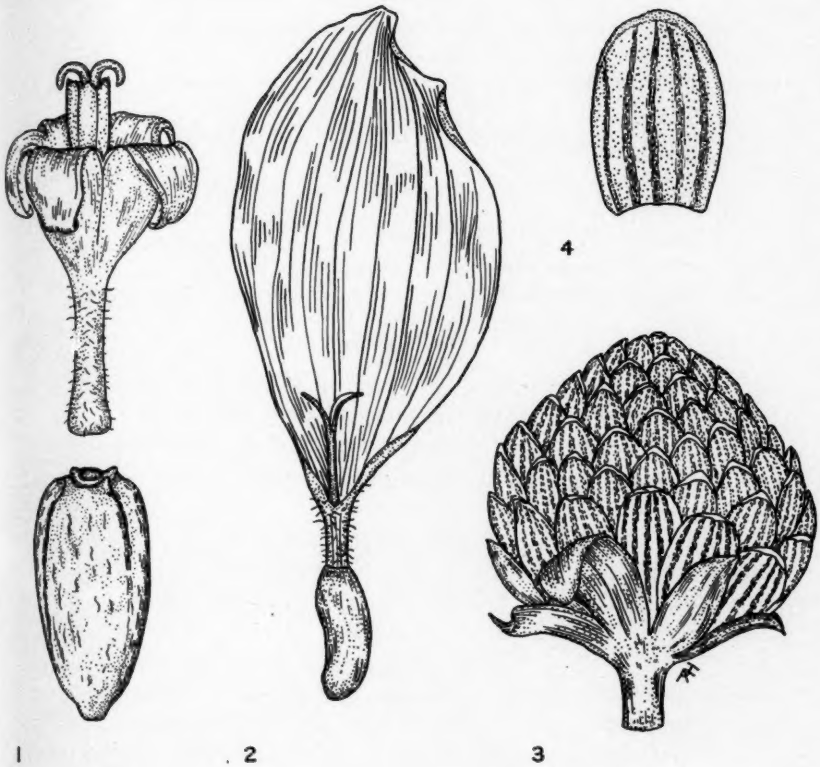
SHARP—EPAPPOSE GENERA OF COMPOSITAE

EXPLANATION OF PLATE

PLATE 6

Greenmaniella resinosa

Fig. 1. Disk-flower, corolla above, achene below. × 9.
Fig. 2. Ray-flower. × 13.5
Fig. 3. Disk, showing the striated pales. × 9.
Fig. 4. Pale, with the scarious apex. × 13.5.



SHARP—EPAPPOSE GENERA OF COMPOSITAE